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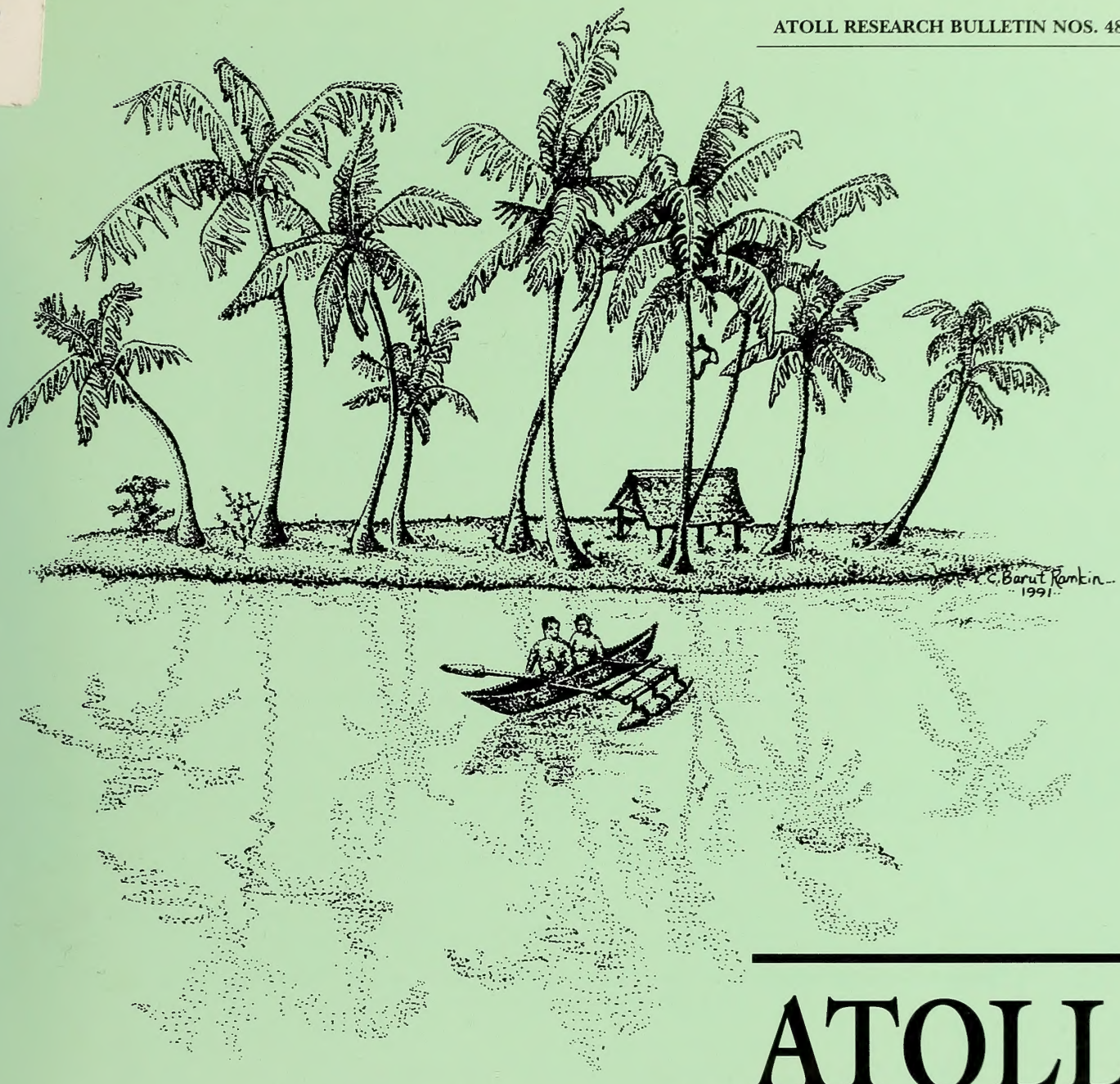

ATOLL RESEARCH BULLETIN

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NO. 481

FIRST PROTOZOAN CORAL-KILLER IDENTIFIED IN THE INDO-PACIFIC

BY

ARNFRIED A. ANTONIUS AND DIANA LIPSCOMB

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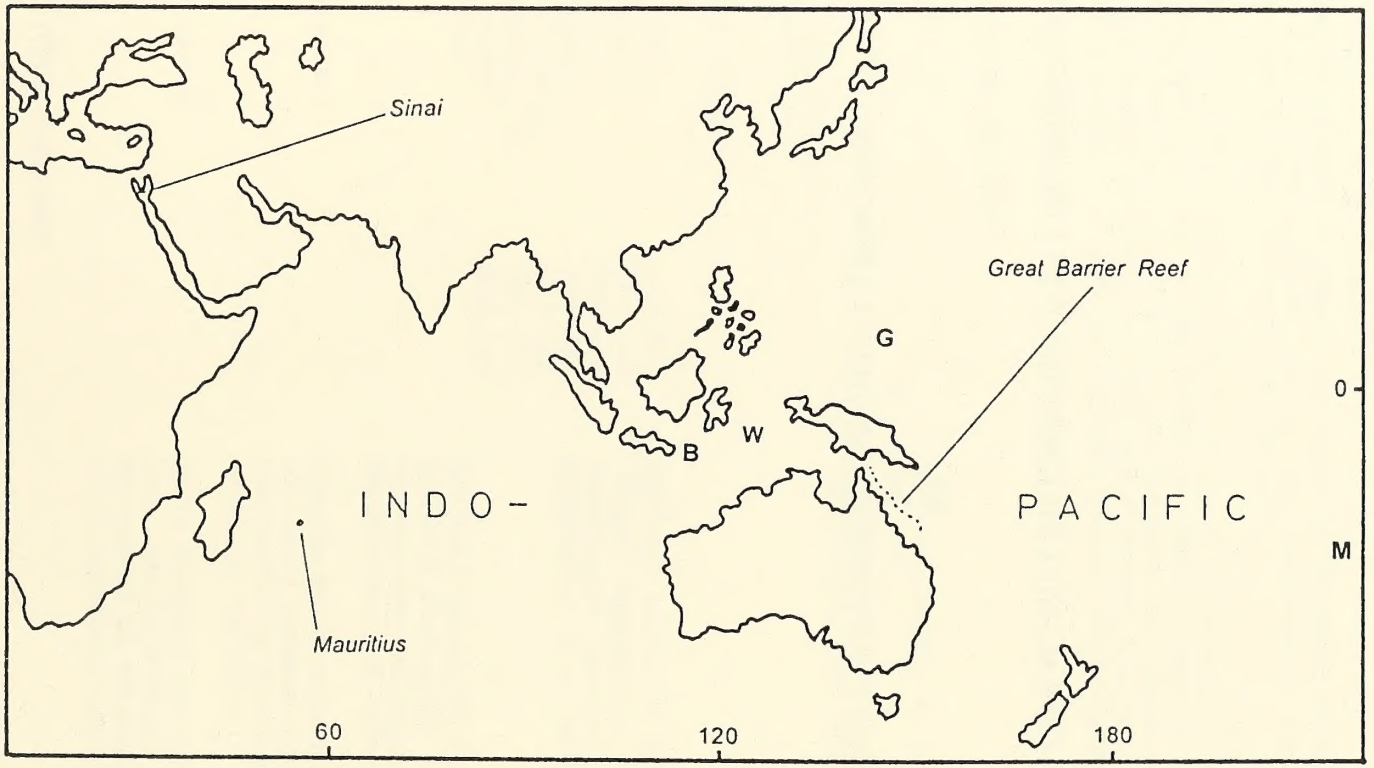

Figure 1. Chart of Indo-Pacific region showing the three SEB observation sites where corals infected with *Halofolliculina corallasia* were investigated: the coral reefs along the coast of Sinai, Red Sea; around the island of Mauritius, Indian Ocean; and in the area of Lizard Island, Great Barrier Reef, Pacific. Motupore Island on the SE coast of Papua New Guinea is not marked on the chart. Sites that were investigated with negative result (no SEB found) are: B: Bali; W: Wakatobi Islands; G: Guam; and M: Moorea.

FIRST PROTOZOAN CORAL-KILLER IDENTIFIED IN THE INDO-PACIFIC

BY

ARNFRIED ANTONIUS[1] and DIANA LIPSCOMB[2]

ABSTRACT

A unique coral disease has appeared on several Indo-Pacific reefs. Unlike most known coral diseases, this one is caused by an eukaryote, specifically *Halofolliculina corallasia*, a heterotrich, folliculinid ciliate. This protist is sessile inside of a secreted black test or lorica. It kills the coral and damages the skeleton when it settles on the living coral tissue and secretes the lorica. Thus, the disease was termed Skeleton Eroding Band (SEB). The ciliate population forms an advancing black line on the coral leaving behind it the denuded white coral skeleton, often sprinkled with a multitude of empty black loricae. This disease was first noted in 1988 and since has been observed infecting both branching and massive corals at several locations in the Indo-Pacific.

INTRODUCTION

More than a quarter century has passed since the first coral-killing syndrome, the Black Band Disease (BBD), was observed in the Caribbean Sea (Antonius, 1973). In the beginning regarded as a rare curiosity rather than a threat, it was soon followed by reports of other deadly syndromes, such as Shut-Down-Reaction (SDR) (Antonius, 1977), microbial infection (Ducklow & Mitchell, 1979), and White Band Disease (WBD) (Antonius, 1981a; and Gladfelter, 1982). All these observations were made in the Caribbean Sea or Western Atlantic (Garrett & Ducklow, 1975; Antonius, 1981b; and Dodge et al., 1982).

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In 1985, a first account was given on coral diseases in the Indo-Pacific (Antonius, 1985a) and an inventory of known syndromes 10 years later (Antonius, 1995a). Thereafter, new deadly syndromes on reef corals were reported in rapid succession, such as *Sphingomonas*-infections (Richardson et al., 1998), Type II WBD (Ritchie & Smith, 1998), Yellow Band Disease (YBD) (Korrubel & Riegl, 1998), *Aspergillus sydowii* damaging Gorgonians (Smith et al., 1996; Nagelkerken et al., 1997; Smith et al., 1998; Geiser et al., 1998; ISRS, 1999; Shinn, 2000; and Weir et al., 2000), and, although not a disease sensu stricto, Tissue Bleaching (TBL) (Glynn, 1993; Adjerout et al., 1995; Kushmero et al., 1996; Brown, 1997; and others). Accounts on reef-deterioration (Antonius, 1998) were given for Western Atlantic (Bruckner & Bruckner, 1997; Antonius & Ballesteros, 1998; and Goreau et al., 1998) as well as Indo-Pacific locations (Riegl et al., 2001). The majority of the responsible diseases appear to be caused by bacterial pathogens (Antonius, 1995a).

We report here the presence of a disease of corals in the Indo-Pacific (Fig. 1) caused by a ciliated protozoan. The progress of the disease is similar to other "band" diseases, such as BBD or WBD (Antonius, 1985b), the infection spreading as a line of pathogenic agents moving over a coral head leaving behind denuded skeletons. Unlike all the other diseases mentioned, which attack the soft tissues of corals, the new syndrome also damages the coral's skeleton. Therefore, we have named it Skeleton Eroding Band (SEB).

The organism associated with the disease is identified as *Halofolliculina corallasia*, a new species of folliculinid, heterotrich ciliate, which makes SEB not only the first known (stony) coral disease caused by a protozoon but also the first caused by an eukaryote.

The first time *H. corallasia* was noted on corals in reefs around Motupore Island, Papua New Guinea was in 1988. Black loricae were seen in microscopic preparations and drawn and photographed (Antonius, pers.obs.), but the phenomenon was not investigated any further. The same year, the syndrome was observed in reefs of Lizard Island, Australia and was listed in transect counts as "BBD-grey" (Antonius, pers.obs.). In 1990, the syndrome was registered as a rare occurrence in reef transects around Mauritius (Antonius, 1993) but its importance was not diagnosed. This finally happened in 1994 during a coral-reef survey in the Gulf of Aqaba, Straits of Tiran, and Ras Mohamed, Sinai, Red Sea (Antonius, 1995c, 1996).

In the following years, all previous observation sites (except Motupore) were revisited in order to investigate the SEB syndrome in detail. In 1998, SEB was mentioned for the first time in an official report (Antonius, 1998), and first photographs were presented in 1999 (Antonius, 1999c). In summer 2000, in order to gather badly needed data on the occurrence of SEB and other diseases (Antonius, 2000a), Pacific locations such as Moorea (Polynesia), Guam (Micronesia), Bali, and Wakatobi Islands (Indonesia) were investigated.

METHODS

Field assessments

Frequency of occurrence of SEB was investigated using a fast-working field technique, the Belt Method (Antonius, 1995b). It is a semiquantitative time-count technique that developed out of routine checks on reef health. Essentially, it is a derivative of visual census techniques that were developed to count reef fishes (e.g. Brock, 1954; Antonius et al., 1978; and Russell et al., 1978) and to assess *Acanthaster* infestations (e.g. Antonius, 1971; and Endean, 1974). While surveying a coral reef, it is relatively easy to note down all cases of active diseases on corals that are encountered. To make this approach semiquantitative merely requires standardization with: (1) a time-frame limiting the duration of each individual survey; and (2) organizing the numbers of every disease encountered into categories.

The time-frame of one single survey is 30 minutes. During this period, the diver swims fairly close to the reef surface and registers all pathologic syndromes on corals in a path, or "belt", about 2 m wide. One such 30-minute survey is considered a "scan". The diver's speed during such a scan may vary. In scarcely populated reef areas and/or reef zones with large coral colonies, the diver will proceed faster and cover more distance than in densely populated reef areas and/or reef zones with smaller coral colonies. However, experience has shown that the total number of coral colonies investigated during one scan remains surprisingly constant (e.g. Antonius, 1988a). In order to assure this consistency, the time count has to be interrupted every time the diver traverses completely barren reef areas.

The categories for the instances of diseases encountered range from zero to six. Zero (0) naturally means no syndrome found. A disease is considered condition: (1) "rare" when 1-3 cases are found during a 30-minute scan; (2) "moderate" when 4-12 cases are found; (3) "frequent" when 13-25 cases are found; (4) "abundant" when 26-50 cases are found (Antonius, 1988a); (5) "epidemic" when 51-100 cases are found; and (6) "catastrophic" at the end of the scale when the number of syndromes exceeds 100, which means that the number of diseases actually become uncountable (Antonius, 1991). (Note: the correct term for a code 5 conditions is "epizootic." This, however, has led to so much confusion with "epizoism" (Antonius & Ballesteros, 1998) that we prefer the unequivocal "epidemic".) The particular numerical values of these six categories have been determined as the most useful based on practical experience during many years of fieldwork. Since the Belt Method is fast and simple to use -- requiring only a watch, a writing slate, and a pencil -- it is very well suited to survey large reef tracts. Under reasonably calm conditions, kilometers of linear reef extension can be surveyed during one day.

Transmission experiments

In order to find out how the SEB syndrome spreads within a given coral population, infection as well as contagion experiments were set up in reefs and in aquaria, following tried methods (Antonius, 1985b). To test infectiousness, SEB-diseased coral colonies were surrounded by three types of target specimens of different coral species: some healthy, some with small injuries, and some with active WBD. At

Sinai and Lizard Island, experimental sample size in reefs consisted of 10 SEB-diseased specimens, each one surrounded by five of these target specimens of different species. Exactly the same arrangement was repeated in aquaria. In Mauritius, an experimental series using 12 SEB-diseased specimens was conducted in reefs alone. To test contagiousness, SEB-diseased specimens were brought into direct contact with healthy ones also representing a variety of species. They were usually tied to each other by very fine fishing lines. Experimental sample size at Sinai and Lizard Island consisted of 10 diseased-healthy coral pairs of varying species in reefs, as well as 10 such pairs in aquaria. In Mauritius, a total of 15 coral pairs were tested in reefs alone.

Pathology

Under the fieldwork conditions of the project, it was not possible to achieve axenic cultures of the pathogen for testing Koch's principle. However, in order to test the influence of possible bacterial synergists on disease behavior, they were removed from the hypothetical SEB consortium by antibiotics. At the Sinai research site, three specimens each of small, infected colonies of *Acropora, Stylophora,* and *Goniastrea* were exposed to the antibiotics penicillin, erythromycin, and gentamycin following a tried procedure (Antonius, 1985a). One gram of the respective antibiotic was tied into a watertight corner of a one-gallon plastic bag. The bag was then put over a small SEB-infected coral, tied at the base, and the antibiotic released. The bag thus contained about two liters of water plus antibiotic, and was removed after 24 hours. Further behavior of these SEB infections was then kept under microscopic observation for about three weeks.

Sample collection

Diseased coral specimens showing the black band of SEB infection were, whenever possible, first photographed *in situ* at the original reef location and then transferred into holding tanks or aquaria for more detailed close-up photography. Live material was also photographed under stereo- as well as research compound-microscopes. These SEB-diseased coral pieces were then fixed in 4% buffered formaldehyde in seawater, individually wrapped in soft plastic bags, and stored and transported in small glass jars filled with preservation fluid. A collection of these samples from Sinai, Mauritius, and Lizard Island is stored at the Institute for Paleontology, University of Vienna, Austria.

Microanatomy

Preserved individuals of *Halofolliculina corallasia* were separated from SEB-diseased coral splinters, embedded in paraffin, sectioned by microtome, transferred to microscopic slides, stained, and preserved under cover slides, generally following methods with a very successful record (Antonius, 1965). Samples are stored at the Department of Biological Sciences, George Washington University, Washington, DC, USA. For documenting the impact of SEB on the coral skeleton, standard scanning electron microscopy techniques were employed. Samples are stored at the Institute for Paleontology, University of Vienna, Austria.

RESULTS

HALOFOLLICULINA CORALLASIA, sp. nov.

Protozoa, Ciliata, Heterotrichida, Coliphorina, Folliculinidae, *Halofolliculina corallasia,* sp. nov.

The species name refers to its appearance on the coral when viewed through a microscope: Greek *lasios* (λασιοσ) means "densely overgrown" or "villous".

Diagnosis

As in other members of the genus *Halofolliculina* (Hadzi, 1951), *H. corallasia* is sessile in a lorica that either lies flattened against the substrate or stands almost upright, in both cases partially embedded in the coral skeleton (Hadzi, 1951). The lorica has an average length of 220 μm (maxima 370 μm, minima 135 μm) and a width of 95 μm (maxima 130 μm, minima 55 μm). The main body within this total length measures an average of 135 μm and the neck, 85 μm. The width of the neck averages 35 μm. The form of the lorica is sac-like with a rounded posterior and a cylindrical neck that angles up from the surface at about 45 degrees (Fig. 7). The neck of the lorica has a single sculpture line circumscribing it. The cell body is attached at its pointed posterior end to the base of the lorica. The cell is large and elongate with two conspicuous pericytostomial wings measuring 175-200 μm when fully extended and bearing the adoral zone of membranelles (feeding cilia). These pericytostomial wings are somewhat unequal in length. The cell is highly contractile and when disturbed retracts completely into the lorica. Two thin flaps of lorica material (one dorsal and one ventral) form an operculum that plugs the opening of the lorica when the animal is contracted (Fig. 8). The somatic cilia are uniform. The nucleus is condensed and oval, rather than beaded. This species differs from other described members of the genus in that the lorica is colored a dark smokey grey to black (clusters of which appear as black spots on the infected coral, Figs. 3 and 4), its size is comparatively small, and it is found infecting corals. A detailed anatomical description of the new species is in preparation (Lipscomb & Antonius, in prep).

Type material

Holotype and paratypes presently are located at the junior author's laboratory, the Department of Biological Sciences, George Washington University, Washington, DC, and will ultimately be deposited in the collections of the Department of Systematic Biology (Invertebrate Zoology), Smithsonian Institution, Washington, DC, USA. The material was isolated from *Acropora downingi* collected in 2 m depth in Mersa Bareika, Ras Mohamed, Sinai.

THE SEB DISEASE

Under the microscope, a live advancing front of *Halofolliculina corallasia* appears as a dense coat of bifurcated beige "tentacles" (pericytostomial wings) emerging from flask-shaped, black loricae (Fig. 5). In this foremost front, loricae often are packed so densely that they form an almost indistinguishable black mass (Fig. 4). Sometimes

their line follows the structure of the coral skeleton, such as the rim of a coral cup or corallite (Fig. 5). In about 10% of all SEB cases encountered in the field, small quantities of nonpathogenic cyanophytes were found dispersed throughout the live SEB front producing the gas bubbles visible in Figs. 3 and 4. They do not change SEB's behavior in any way. The basal part of each lorica is embedded in the spongy, trabecular structure of the coral skeleton, which is broken up into splinters by the ciliate. When observing live material, the slightest jolt makes all protist retract instantly into the loricae but, after only half a minute or so, they will slowly reappear extending their bifurcated wings, resembling a bed of microscopic garden eels to the eye of a diver (Fig. 5).

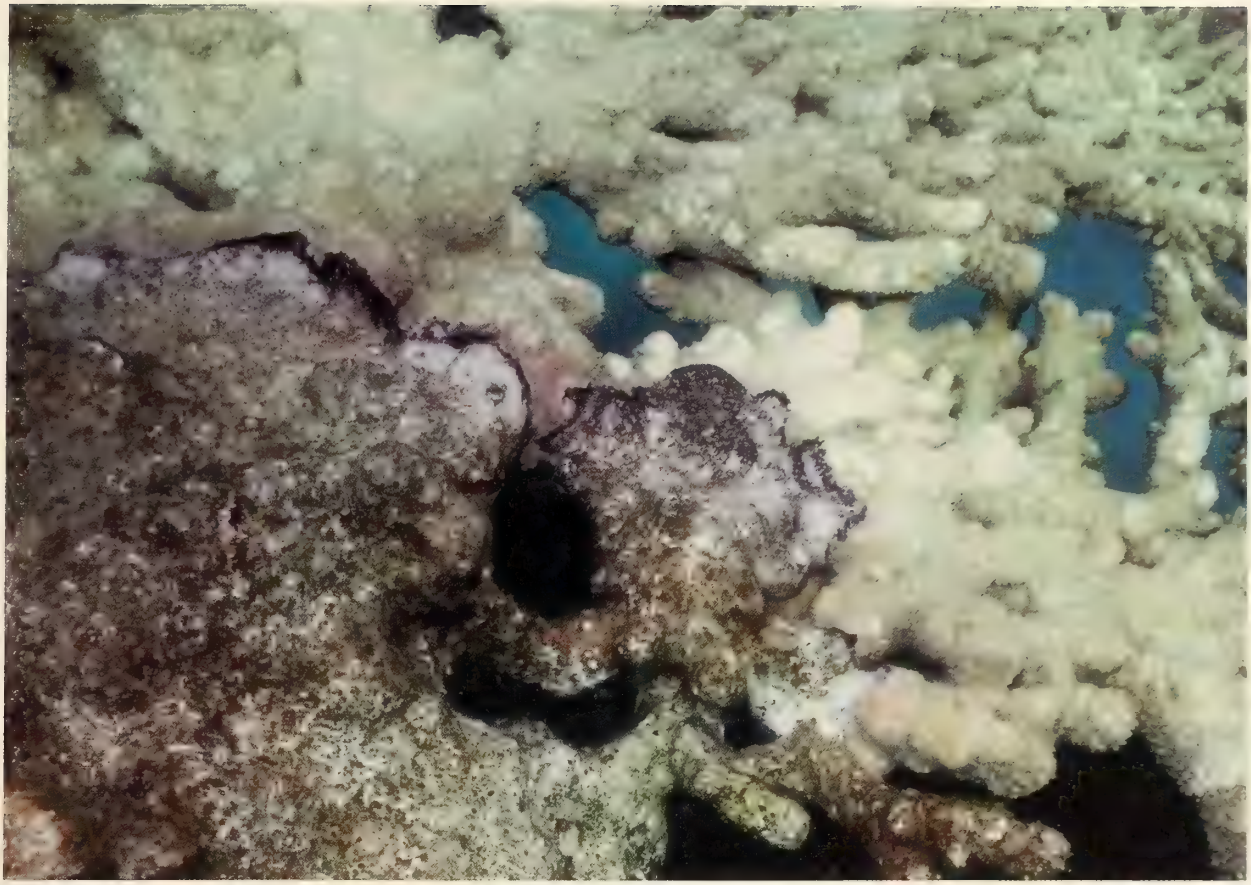
Upon cell division (asexual reproduction) vermiform, migratory larval stages, are produced. These ciliated larvae scout the terrain ahead of the SEB band and locate a suitable spot not too far from this band (Fig. 4). There they penetrate the living coral tissue (which appears unharmed up to this moment), settle down in clusters (Fig. 4), and secrete pseudochitinous loricae which are shaped by the rapid spinning of the larvae. It is the chemicals associated with the unhardened lorica, combined with the mechanical disruption caused by the spinning larvae, that appears to damage the coral skeleton (Antonius, 2000 b) and initiates lysis of the coral tissue. The mechanics of this process can be observed clearly on live material under the microscope. As a consequence of these processes, not only is the coral tissue gone once infection has passed over an area, but the bare coral skeleton has lost all fine structure, its surface looking like a microscopic rubble field (Fig. 6). When viewed with scanning electron microscopy, the rounded imprints of the tips of loricae are clearly visible (Fig. 6). Interestingly, coral polyps appear unharmed ahead of the advancing front of destruction (Fig. 4). SEB does not fall into the recently described category of epizoism syndromes (Antonius & Ballesteros, 1998; and Antonius, 1999a, b) but represents a genuine disease forming an advancing front which leaves behind a naked skeleton (Antonius, 1981a, 1988b; and Richardson et al., 1998).

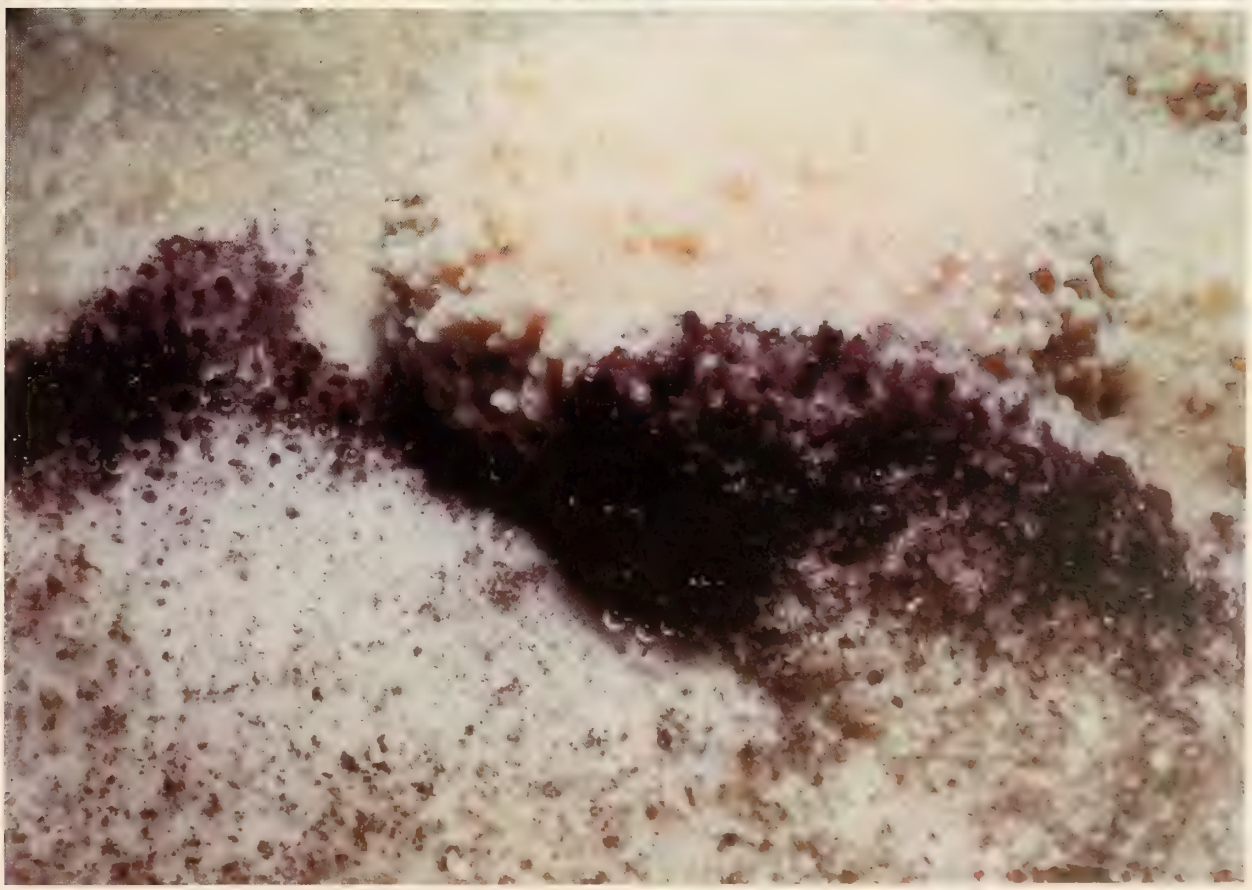
Figure 2. (Opposite page above.) Underwater photograph of a 3 m-diameter colony of *Acropora downingi* with a very large SEB infection in Mersa Bareika, Ras Mohamed, Sinai. The black band of pathogenic *Halofolliculina corallasia* separates live coral tissue (above right) from denuded skeleton (below left). The older, tissue-stripped parts of the skeleton at the left bottom of the picture are overgrown by algal turf.

Scale: entire width of photograph at bottom = 80 cm.

Figure 3. (Opposite page below.) Close-up photograph of the same SEB infection as depicted in Fig. 2. The black front of coral-killing *Halofolliculina corallasia* proceeds upward towards the living coral tissue. The surface of the coral skeleton in the rear of the black band, freshly stripped of coral tissue (below), is sprinkled with tiny black dots consisting of clusters of empty loricae of the ciliate. This "dotted" zone distinguishes the SEB syndrome from the well-known BBD.

Scale: entire width of photograph = 8 cm.





Ecology

SEB occurs in sheltered, lagoon-type environments at a depth of 0 m to at least 35 m (Winkler, in prep.), showing the greatest abundance at depths between 0.5 m and 3 m. In this shallow range, up to 5% of any given coral species can be infected with the ciliate. SEB was found throughout different seasons of the year: April, May, September, and October around Sinai and Aqaba (Red Sea, Fig. 1); April, September, and October around Mauritius (Indian Ocean, Fig. 1); January, February, and August around Lizard Island (Pacific, Great Barrier Reef, Fig. 1); and June, July around Motupore Island, SE Papua New Guinea (Pacific, Fig. 1). Thus, SEB, occurring through warmer and cooler periods in roughly equal concentrations, does not seem to be seasonal.

SEB infects and damages a wide variety of branching and massive reef corals, including the species *Stylophora pistillata, Pocillopora damicornis, P. verrucosa, P. eydouxi, Montipora monasteriata, Acropora aspera, A. humilis, A. formosa, A. noblis, A. tenuis, A. valida, A. florida, A. hyacinthus, A. clathrata, A. downingi, Leptoseris explanata, Pachyseris rugosa, Hydnophora microconos, Favia stelligera, Favites abdita, Goniastrea retiformis, Leptastrea purpurea, Cyphastrea chalcidicum,* and *C. serailia.*

Symptoms of the disease vary. It may appear as thin lines of not more than 1 mm in width (e.g on *Stylophora pistillata*) or as thick, black bands up to 10 cm wide, encircling dead coral surface areas of 80 cm in diameter (e.g. on *Acropora downingi*) (Fig. 2; = *A. cytherea* in Antonius et al., 1990). In contrast to ordinary BBD, which leaves behind a zone of unblemished, brilliant white coral skeleton (Antonius, 1981a), the white coral skeleton immediately behind the advancing front of SEB shows a multitude of tiny black dots that are clusters of flask-like, black housings (loricae) of the ciliate (Figs. 3 and 4) left behind. SEB infections can be almost stationary, moving perhaps 1 mm per week, or comparatively fast, progressing more than 1 mm per day, resembling the behavior of BBD (Antonius, 1988b). The syndrome occurs rather evenly distributed in reef-crest areas, with no apparent tendency to form clusters.

Figure 4. (Opposite page above.) Underwater macrophotograph of the same SEB infection as shown in Fig. 2 and Fig. 3. The front moves from left to right. The rear of the black band (left) shows the usual "sprinkled" or "dotted" appearance, while in front of it (right) partly contracted, but totally unharmed, polyps are visible. The finger-like protrusion of the black band at upper right is a cluster of "scout" larvae of *Halofolliculina corallasia* penetrating the coral tissue, producing loricae and becoming sessile.

Scale: entire width of photograph = 18 mm.

Figure 5. (Opposite page below.) Microphotograph of *Halofolliculina corallasia* on a corallite of *Acropora aspera* at Lizard Island. The bifurcated, beige, pericytostomial wings of the animals are fully extended, emerging from vase- or flacon-shaped black loricae. The basal part of every lorica is embedded in the coral skeleton, producing the specific erosion of the surface typical for SEB.

Scale: entire width of photograph = 1.8 mm.

In some of the reefs under observation, frequency of occurrence of SEB has definitely been increasing over the years. It went from a code 1 (rare) to a code 3 (frequent) level (Antonius, 1995b) in the Rivière Noire area of SW Mauritius (Antonius, 1993) between 1990 and 1998. Exactly the same, a rise from code 1 to code 3, happened in Sinai in only three years (Antonius, 1998) from 1994 to 1997. Only in the reefs surrounding Lizard Island was the change very slight. It took SEB 10 years, from 1988 to 1998, to achieve a rise from a code 1 (rare) to a code 2 (moderate) frequency of occurrence.

Biogeography

As mentioned above, SEB has been found, observed, and investigated in the Red Sea and at Mauritius in the Indian Ocean as well as on the SE coast of Papua New Guinea and the Great Barrier Reef in the Pacific. Since the disease definitely occurs from the western end of the Indian Ocean to the western rim of the Pacific, an attempt was made to document SEB in other locations of the Pacific Ocean as well. Thus, reefs around the islands of Moorea (Polynesia), and around Guam (Micronesia) were investigated as well as many reef sites throughout the Wakatobi archipelago southeast of Sulawesi (Indonesia). Except for frequent epizoism by *Pneophyllum conicum* (the PNE syndrome, Antonius, 1999b), these reefs were found to be relatively healthy and no SEB whatsoever was observed. Because human-related impact on all these reefs was considered minor, an effort was made to survey reefs in Nusa Dua Watersport Bay, one of the most heavily impacted marine environments of Bali. Reef outcrops in this bay are exposed to turbidity, sewage, divers, and boat anchors, to mention just the major sources of stress. But still, not a single case of the SEB syndrome was found.

In order to gather data on Western Atlantic reef areas, a concentrated search for SEB was conducted during winter, spring, and summer seasons of 1997-2000 in the impacted reefs of Belize, Central America, and in the very sick reefs of the Florida Reef Tract and the surprisingly healthy reefs of the Dominican Republic. The result was equally negative at all three locations. Thus, it appears that SEB does not occur in the Caribbean Sea (Antonius, 2000a). To date, no data exist on Eastern Atlantic or Eastern Pacific reef areas. Present data on occurrence or absence of SEB are depicted in Fig. 1.

Pathology

Infection experiments, following tested methods (Antonius, 1985b), were inconclusive perhaps due to insufficient observation time or inability to reproduce the exact conditions that cause new infections. Freshly collected corals, some with active WBD and/or artificial injuries (see Methods) and placed in aquaria with freshly collected SEB-diseased ones did not get infected over a time span of one month. Only once, at Lizard Island, after three weeks of exposure, did a WBD-afflicted *Favia stelligera* contract SEB. The same arrangement set up in reefs at all three research locations did not produce any positive results during observation periods of one month. *Stylophora, Pocillopora, Acropora, Favia,* and *Goniastrea* species were used in these experiments.

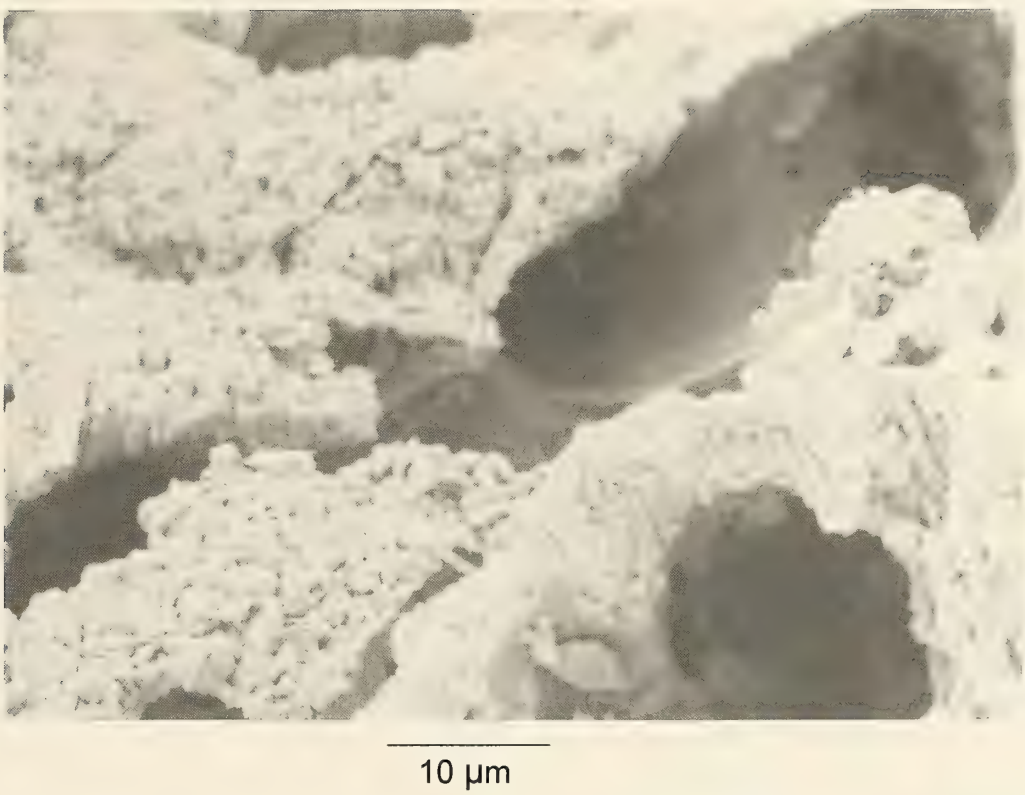


Figure 6. SEM photograph of a septum of *Cyphastrea chalcidicum* from Mauritius showing the typical etched-out holes where the posterior ends of loricae of *Halofolliculina corallasia* were partially embedded in the coral skeleton. Clearly visible is the very smooth surface inside the holes as well as the tiny splinters surrounding them broken loose in the process of excavation. These skeletal fragments make corallites and coenosteum appear like microscopic rubble fields. The term "Skeletal Eroding Band" (SEB) of the disease derives from this characteristic.

Contagion experiments were more successful. When diseased parts of one coral were brought into contact with the healthy surface of another one, the target showed first signs of SEB within one week. Only branching growth forms, such as *Stylophora, Pocillopora,* and *Acropora* species, were used in these experiments which were 100% successful in aquaria at Sinai and Lizard Island. In reefs of all three research sites, 90% of experiments were positive in which the two corals, donor and target, remained in contact. Despite being tied to each other, wave action or other disturbances sometimes separated these pairs. Successful transmissions, regardless of the combination of coral species used, resembled experimental results with BBD (Antonius, 1985b).

Several SEB infections that were made bacteria-free with antibiotics (Antonius, 1985a) were subsequently examined under stereo- and research-microscopes over periods of about three weeks. It turned out that behavior and virulence of *Halofolliculina corallasia* remained identical before and after treatment. In all "disinfected" samples, SEB fronts advanced at the same speed as before, producing scouting larvae, clusters of new loricae, erosion of coral skeleton, and lysis of coral tissue. It seems that SEB's pathogenicity and virulence are caused by *H. corallasia* without the aid of bacterial synergists.

DISCUSSION

None of the other 31 genera in the family Folliculinidae, nor the other species of the genus *Halofolliculina*, are known to cause diseases in corals or any other animal. The members of the family, however, are all sessile in loricae which may be attached to aquatic plants or invertebrates, primarily in the marine environment (Corliss, 1961). Among these, *Halofolliculina corallasia* is the only species known to date acting as a true pathogen on reef corals, an activity directly observable on live material under the microscope. In the reef areas under observation, the SEB disease caused by *H. corallasia* has certainly become more frequent and conspicuous over the past several years. The reason for this may be found in generally worsening conditions in coral-reef environments (Ginsburg, 1993; and Wilkinson, 2000). Under these conditions, increasingly virulent coral diseases not only open up the gateways for infection (Antonius, 1985b), but decaying coral tissue produces bacterial blooms (Mitchell & Chet, 1975) which are food for Folliculinids (Andrews, 1946; and Laakmann, 1903) such as *H. corallasia*. The result may well be population explosions of *H. corallasia* which subsequently lead to SEB infections on reef corals. Lysis of the coral tissue by the SEB disease most probably attracts further swarms of bacteria on which *H. corallasia* feeds, thus in an indirect way converting coral tissue into nourishment. A veritable *circulus vitiosus* thus could be initiated, leading to more infections and spreading of SEB disease in the coral population. These hypothetical conditions, however, could not be produced in the limited field working time of the project. Pathogenesis of primary infections, therefore, really could not be clarified by experiments fitting the time-frame available. Clearly, much more research is needed. In comparison, research on BBD has gone on for almost 30 years (Antonius, 1973) and is still in progress.

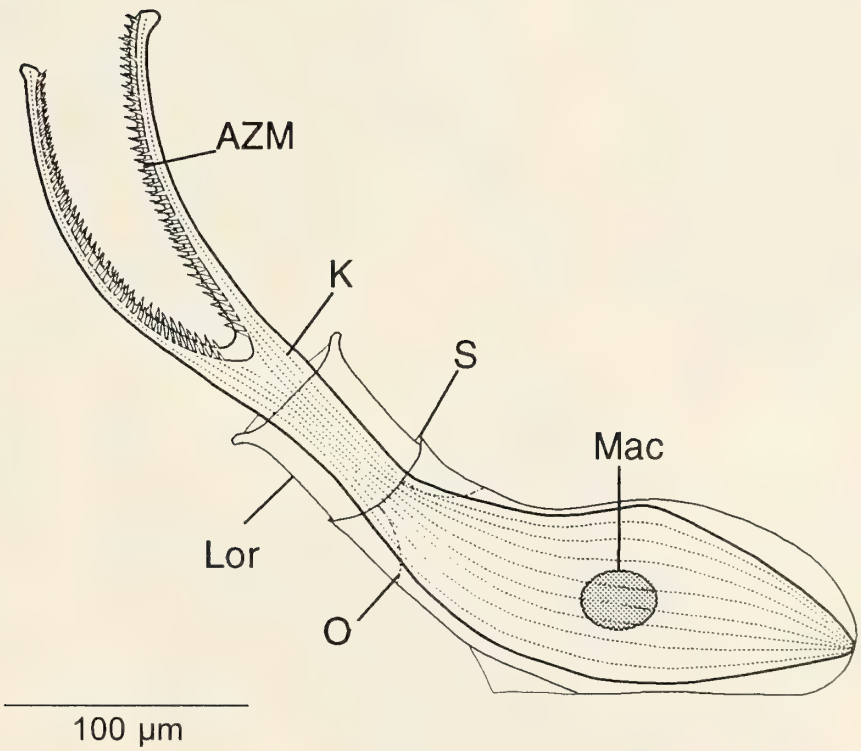


Figure 7. Drawing of *Halofolliculina corallasia* showing the major distinguishing features. The adoral zones of membranelles (AZM) line the two pericytostomial wings and create water currents that direct food into the cell mouth. The cell body sits inside a lorica (Lor), which has a sculpture line (S) around the neck, and an operculum (O) that closes off the lorica when the cell has contracted. The macronucleus (Mac) is spherical rather than beaded. Body cilia lie in rows called kineties (K).

The tendency of Folliculinids to form massive aggregations on a wide variety of substrates has been known for a long time and has been depicted variously by Andrews in excellent drawings (Andrews, 1914, 1915, 1923, 1949). All these species are epibenthic to epizoic, completely harmless and nonpathogenic. The unusual pathogenic behavior of *H. corallasia* may have developed in a way termed "Xenökie" by Hadzi (1935), who observed several different species of Folliculinids sitting with the posterior end of their loricae in the empty chambers of individual bryozoans. They did not appear to harm any live bryozoans, but this kind of behavior may well constitute the first step toward pathogenicity. As so many other pathogens do (Antonius, 1985a, 1988b; Antonius and Ballesteros, 1998; and Verlaque et al., 2000), *H. corallasia* may have learned to invade living coral tissue from the secure foothold of adjacent bare-skeleton surfaces. Interestingly, coral polyps immediately ahead of an advancing front of SEB appear undisturbed (Fig. 4), an observation also made on BBD infections more than a decade ago (Antonius, 1988b; figs. 3, 4, 5). The special surface-eroding anchoring of the lorica then possibly could have developed in response to the push-and-pull of the surrounding living (but doomed) coral tissue. How this process erodes the coral surface, produces the microscopic "rubble fields", and starts lysis of the coral tissue can be directly observed on live material. No secondary microborers are involved here. This specific type of damage and boring that *H. corallasia* inflicts to the surface of the coral skeleton (Antonius, 2000b) might also be preserved and recognizable in the fossil record (Golubic et al., 1975; and Falces, 1997).

CONCLUSIONS

SEB, up to now, has been documented on exactly 24 Indo-Pacific coral species, a number that is bound to increase in the future. So far, it has not been found in Atlantic and Caribbean waters, i.e., outside of the Indo-Pacific zoogeographic region (Antonius, 2000a). In the Indo-Pacific, the pattern of occurrence is somewhat complicated and not easy to understand. In the western Indian Ocean the disease was found at the northern (Red Sea) and southern (Mauritius) limits of reef development, but towards the eastern extreme, where Indic and Pacific waters merge (Bali, Wakatobi Islands), SEB does not seem to occur. Another 30° to the east, roughly along the 145° E meridian, SEB was found south of the equator (Great Barrier Reef, Papua New Guinea) but not in the north (Guam). Toward the eastern margin of the West Pacific (Moorea, 150°W, 17°S) SEB also seems to be absent. This confusing picture clearly needs input by more than one fieldworker. Thus, in order to clarify questions of occurrence and distribution and also to quantify the impact of SEB on coral reefs on a wider scale, marine biologists must learn to distinguish SEB from BBD (Antonius, 1999c). In our discussions with on-site scientists, we have learned that SEB usually was mistaken for BBD. SEB may have been scarce and hard to find in the past but, at least in the observation areas discussed here (Fig. 1), it passed the "threshold of noticeability" a decade ago. Our present field data on occurrence of SEB, collected on a relatively small scale but over a time span of about 10 years, suggest that its frequency of occurrence is increasing, adding substantial impact to the rising tide of coral diseases (Antonius, 1995d; Goreau et al., 1998; Richardson, 1998; Epstein, 1998; Hayes and Goreau, 1998; Harvell et al., 1999; and Porter et al., 1999).

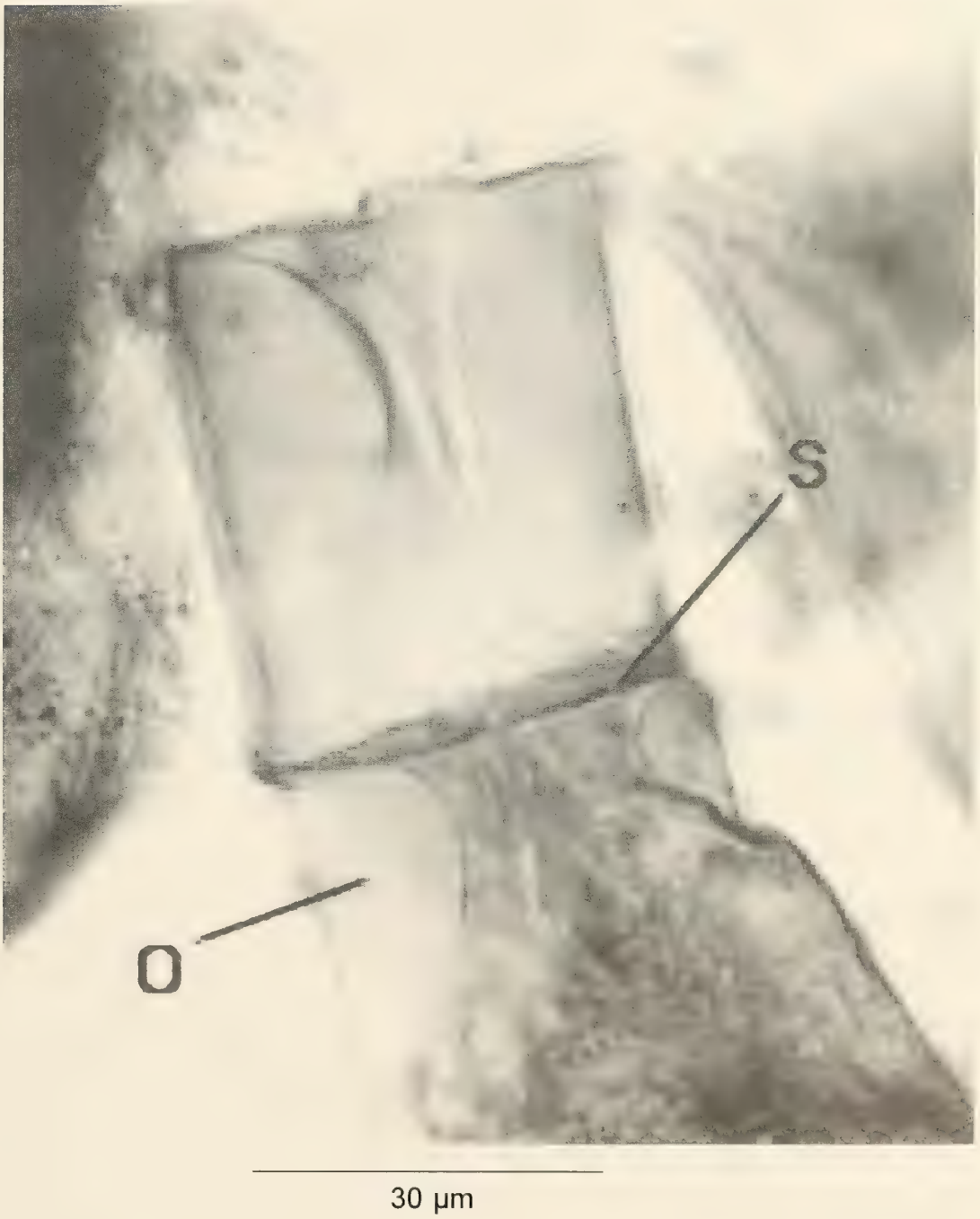


Figure 8. Microphotograph of an empty lorica of *Halofolliculina corallasia* showing the suture line (S) and the operculum (O) that closes the opening when the cell is contracted.

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Note: In March 2001, an interesting observation was made at the Jordanian fertilizer port, close to the Saudi Arabian border (Gulf of Aqaba, Red Sea), which proved to be the most heavily polluted of all Jordanian research sites (Winkler, in prep.).

Several colonies *Echinopora gemmacea* and *Echinophyllia aspera* of about 1 m in diameter were attacked by extremely massisve and virulent SEB infections and killed entirely within a time span of just one week (Caitriona McInerney, pers. comm.).

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ATOLL RESEARCH BULLETIN

NO. 482

SEABIRDS OF THE CAMPECHE BANK ISLANDS, SOUTHEASTERN GULF OF MÉXICO

BY

JOHN W. TUNNELL AND BRIAN R. CHAPMAN

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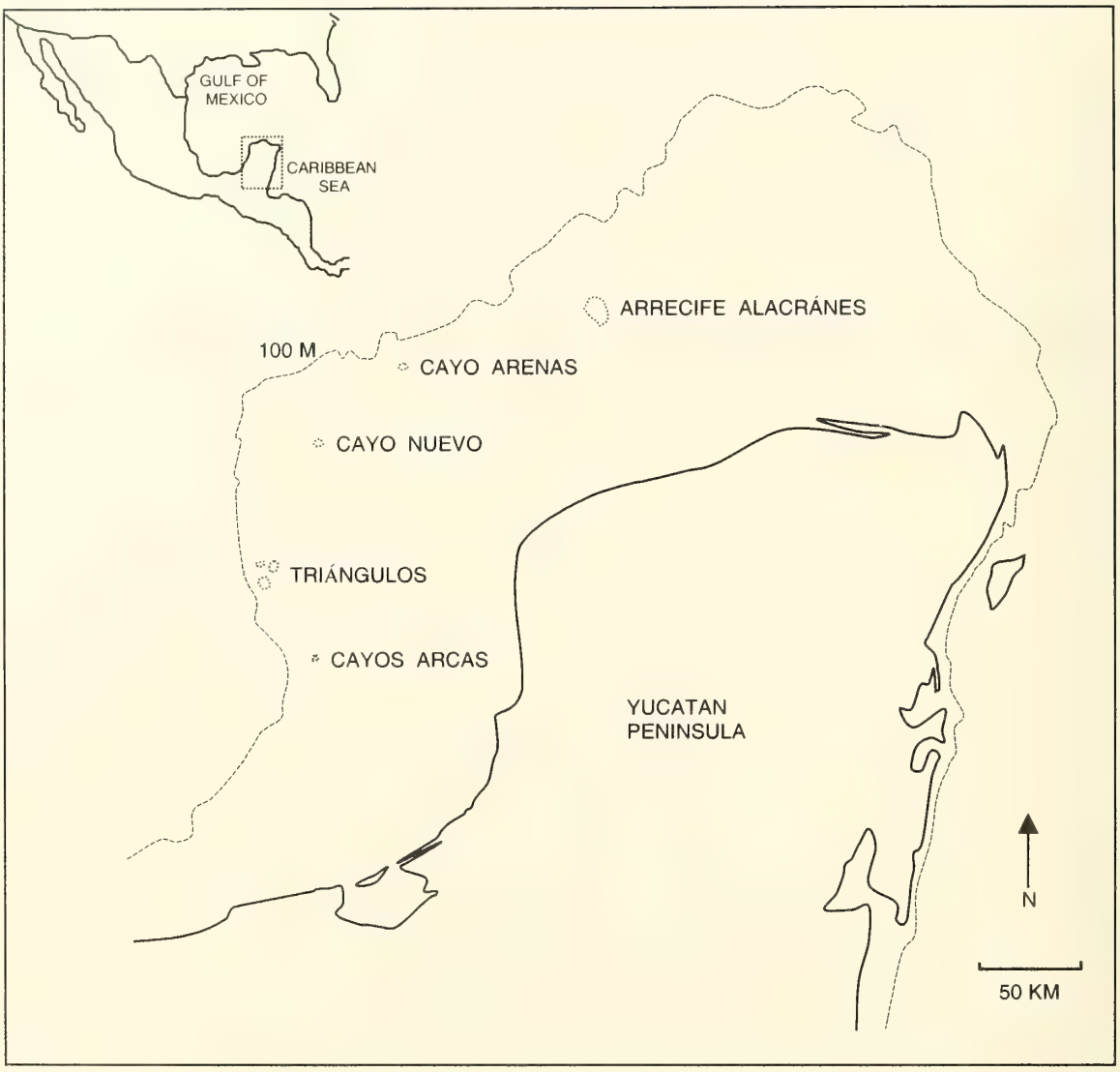

Figure 1. Location of reef island complexes on the Campeche Bank of the southeastern Gulf of México.

SEABIRDS OF THE CAMPECHE BANK ISLANDS, SOUTHEASTERN GULF OF MÉXICO

BY

JOHN W. TUNNELL, JR.[1] and BRIAN R. CHAPMAN[2]

ABSTRACT

Seabirds of the Campeche Bank islands in the Gulf of México were surveyed during 1986. Eight of 12 permanently emergent islands had active seabird nesting colonies during the study period from winter through summer. Nine species of colonial seabirds nested on the islands: Masked Booby, Brown Booby, Red-footed Booby, Magnificent Frigatebird, Laughing Gull, Royal Tern, Sandwich Tern, Sooty Tern, and Brown Noddy. Descriptions of colony locations in relation to vegetation or other island features along with bird censuses and historical records are presented. These large seabird populations in the southern Gulf of México appear to have remained fairly stable, and they should be surveyed on a regular basis and protected.

INTRODUCTION

The Campeche Bank, an extensive submarine continuation of the limestone plateau that forms the Yucatán Peninsula (Macintyre et al. 1977), extends for about 650 km along the western and northern coasts of the Yucatán in the southeastern Gulf of México. The bank is characterized by relatively shallow waters with many shoals and coral reefs, but few emergent islands. Within the Campeche Bank there are only four groups of islands (Figure 1) that are large enough and sufficiently elevated to support terrestrial floras and faunas. These groups are known as Arrecife Alacránes (22° 23' N, 89° 40' W), Cayo Arenas (22° 07' N, 91° 24' W), Arrecifes Triángulos (20° 58' N, 92° 20' W), and Cayos Arcas (20° 13' N, 91° 58' W). A fifth, Cayo Nuevo (21° 50' N, 92° 04' W), consists of a low, barren sand cay that probably is inundated by storm tides and wave action and a submergent reef flat that may be exposed during extremely low tides. All of the islands in these groups are located more than 120 km from the mainland and rarely are visited by recreational boaters or fishermen, although considerable numbers of commercial fishermen regularly visit some of the islands, primarily the Alacránes and Arenas groups. All four of the main island groups have lighthouses that are staffed by keepers, and sometimes their families and pets. Some of the islands (Arcas group) also facilitate crude oil storage and transfer facilities by *Petroleos Mexicanos* (PEMEX), the national oil company of México, and are guarded by small (2-4 men) Naval detachments. Each island group has a Naval weather station.

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Geologic and topographic features (Kornicker et al. 1959, Fosberg 1961, Folk 1967, Macintyre et al. 1977, Wells 1988), submarine fauna (Kornicker et al. 1959, Kornicker and Boyd 1962, Farrell et al. 1983, Chávez et al. 1985) and terrestrial flora (Millspaugh 1916, Bonet and Rzedowski 1962) of certain Campeche Bank islands have been described, but terrestrial fauna of the islands has not been well documented. Much of the information about seabirds that visit or nest on the Campeche Bank islands must be gleaned from anecdotal accounts in cruise reports, geologic explorations, or floristic surveys. Although there have been several recent accounts of marine birds on the Campeche Bank reefs (Paynter 1955, Boswall 1978, Tunnell and Chapman 1988, Howell 1989, Lockwood 1989), thorough surveys of the seabird populations apparently have never been made during the probable period of peak nesting (Clapp et al. 1982).

The first account of the seabird colonies on the Campeche Bank islands was written by the English adventurer Dampier (1699), who first visited the area in 1675. Nearly two centuries passed before the avifauna of the islands north of the Yucatán Peninsula was again mentioned by Smith (1838), Marion (1884), Ward (1887) and Agassiz (1888). A British Navy officer visited two of the smaller islands in Alacrán Reef (islas Pájaros and Chica) in mid-May 1912, and provided the first indication that the Campeche Bank islands might be significant nesting areas for tropical terns (Kennedy 1917). However, these early accounts were based upon brief visits to one or two islands of a single reef and the avifauna of the islands remained poorly documented until the early 1950's.

During a survey of the birds of the Yucatán Peninsula, Paynter (1955) landed on four islands in 1952 and became the first scientist to describe the colonies of marine birds on more than one of the reef complexes. Although his visits to the islands were made during August and September, probably too late to observe the peak of nesting, Paynter found a few active nests of some species and speculated upon the extent of the colonies. Large flocks of many species remained in the area and the remnants of recently abandoned nests were evident. Interestingly, both Paynter (1953, 1955) and Siebenaler (1954) visited or anchored near several of the Campeche Bank islands in August and September, 1952, but Seibenaler did not mention the presence of nesting seabirds or the existence of seabird nests. Both of these researchers were recording the presence of avian species engaged in trans-Gulf migration.

Kornicker et al. (1959) were on Alacrán Reef in June 1959, but focused their attention on the marine features of the reef. They listed the birds that were seen nesting on the islands without providing information on avian numbers or colony locations. Alacrán Reef was examined again in August and September 1975 by Boswall (1978), who summarized most of the published information on the marine birds of the reef.

The IXTOC I oil spill in the Bay of Campeche focused renewed attention on the seabird colonies in the southern Gulf of México. The spill, which began on 3 June 1979, occurred when an offshore drilling rig blew out at a location just 75 km from a known seabird colony on Cayos Arcas (Clapp et al. 1982). Oil from IXTOC I flowed continuously until March 1980, and an estimated 3.3 billion barrels of oil were released into the Gulf of México (Woods and Hannah 1981). Although few oiled seabirds were recovered along the

Texas coast after the spill (Chapman 1981), the islands of the Campeche Bank were apparently never checked while oil was contaminating the waters of the Gulf (Clapp et al. 1982). The probability was high that many nesting birds were oiled because of the timing of the spill. Duncan and Havard (1980) determined that many species of pelagic birds regularly frequent the northern Gulf of México, an area that was heavily impacted by the spill. Consequently, Clapp et al. (1982) urged that seabird populations in the Gulf of México be surveyed.

Between January and July 1986, one of us (JWT) visited all four coral reef complexes, including 12 islands, on the Campeche Bank. Since some of the islands were visited during the probable peak of the seabird breeding season, we censused the nesting birds on each island and surveyed their colony locations relative to vegetative and topographic features. Although our visits to some islands likely did not coincide with the peak of the nesting season, we are providing the most comprehensive description of the avifauna on the Campeche Bank islands available to date. We suggest that colonies of nesting seabirds are much larger and more widely dispersed among the islands than previously believed. Furthermore, since Alacrán was recently designated as a protected area (Parque Marino Nacional Arrecife Alacránes) and the other Campeche Bank islands are under consideration for protection, we recommend monitoring and conservation programs be developed to sustain these populations as some of the most extensive seabird nesting colonies in the Gulf of México.

STUDY AREA

The Campeche Bank extends seaward into the Gulf of México 190 to 290 km beyond the northern shoreline of the Yucatán Peninsula. The continental shelf slopes gently from the shoreline to the shelf-slope edge at an overall gradient of approximately 0.5 m per km. The submerged plateau is bordered on the west, north and east by steep slopes which drop from depths of 80-220 m at the shelf-slope edge to the abyssal zones of the Gulf of México. Three major submerged terraces are superimposed upon the bank and occur at depths of 90-110 m, 50-64 m, and 30-37 m (Logan 1962, 1969). A succession of rocky knolls are aligned along the shallowest portions of the 50-64 m terrace and form an almost continuous raised rim around the western and northern margins of the Campeche Bank. Although most of these knolls form topographic highs reaching elevations of 15-45 m below present sea levels, communities of hermatypic corals, encrusting and nodule-forming coralline algae and foraminifera colonize the flanks of some knolls, raising reefs and reef-banks to the surface. Four of these coral reef complexes have low islands (cays) of coral rubble or sand on their tops. These reef complexes consist of 15 permanently emergent islands, 12 of which are vegetated.

The island-reef complexes of the Campeche Bank consist of low islands encircled by shallow-water sand flats, seagrass meadows and reef flats. The reefs are surrounded by clear, tropical oceanic water that flows from the Caribbean Sea into the Gulf of México. Currents generally run from the east or northeast at all Campeche Bank reef complexes, but during the period from November to February, "*nortes*" (winter cold fronts) occasionally reach the area and generate strong winds, wave energy and surface currents from the north.

During most of the year, the prevailing winds are easterly, varying from northeast to southeast, and tidal ranges are minimal, fluctuating from 0.6m to 1.0 m (Wells 1988). Surface water temperatures in the area range from 29° to 30° C during the summer to a minimum of 24° C in the winter (Logan 1969). Brief descriptions of each reef-island complex and their habitats are given below.

Arrecife Alacránes

Alacrán Reef is the largest (25 x 13 km) and most well known of the Campeche Bank reef formations (Kornicker et al. 1959, Fosberg 1962, Kornicker and Boyd 1962, Hoskin 1963, 1966, Bonet 1967, Folk 1967, Chávez et al. 1985, Wells 1988). The Alacrán atoll platform, located approximately 137 km north of Progreso, Yucatán, has five sand cays on its leeward margin (Figure 2). All of the islands are low-lying and their outlines vary seasonally with storms and changing wind directions (Kornicker et al. 1959). The cays support abundant vegetation (Millspaugh 1916, Bonet and Rzedowski 1962, Fosberg 1962) and seabird nesting colonies (Boswall 1978). The larger islands, islas Perez, Desertora, and Desterrada, are situated on the leeward shelf of the reef, whereas islas Chica and Pájaros are located on the southern tip of the inner reef flat. Isla Desterrada was once cut apart by a storm to form islets, East and West Desterrada (Fosberg 1962), that have since rejoined. A sand bar, called Desaparecida Bar, usually is emergent on the middle part of the leeward reef shelf during the summer months, but is eroded by wave action and disappears with the onset of northerly winds. Isla Perez, the largest of the cays (150 m x 870 m), is the only island on Alacrán Reef that has been altered by human activity. The island has a manned lighthouse and weather station and several abandoned buildings that are occasionally occupied by visiting fishermen. Isla Desterrada has an automated light. Some of the islands have local names (in parenthesis) that may cause confusion because they appear in some earlier reports: Desterrada (Utowane); Desertora (Allison; Muertos); and Pájaros (Blanca).

Cayo Arenas

Three reef masses on the northern margin of the continental shelf form the Arenas reef group which consists of four emergent islands (Logan 1969). Three of the emergent islands on this reef are unnamed (Figure 3A). These islands are small, unvegetated and composed primarily of coral rubble (Chávez et al. 1985). Only one island on this reef, Cayo Arenas, is large and elevated enough to support permanent vegetation. The island, which measures 240 m x 275 m across its widest points, is composed of sand in the central and leeward (westward) portions, but the substrate on windward side is mostly coral rubble and solidified beachrock (Busby 1966). A manned lighthouse and weather station are centrally located.

Cayo Nuevo

Nuevo reef is a small reef knoll located on the northwestern margin of the Yucatán shelf (Logan 1969). Cayo Nuevo is a small, crescent-shaped sandy island that sits atop a limestone prominence. The cay remains barren because it is frequently inundated by storm

Figure 2. Map of Arrecife Alacránes (Alacrán atoll) showing reef islands on leeward margin.

waves and abnormally high tides. The low-lying island may serve as a roosting and loafing area for birds, but it may be too ephemeral to serve as a nesting area.

Arrecifes Triángulos

The Triángulos reef group is the smallest and least known of the four major Campeche Bank reef-island formations (Chávez 1966, Logan 1969, Chávez et al. 1985). The reef group consists of two submerged ridges each with emergent islands that are located

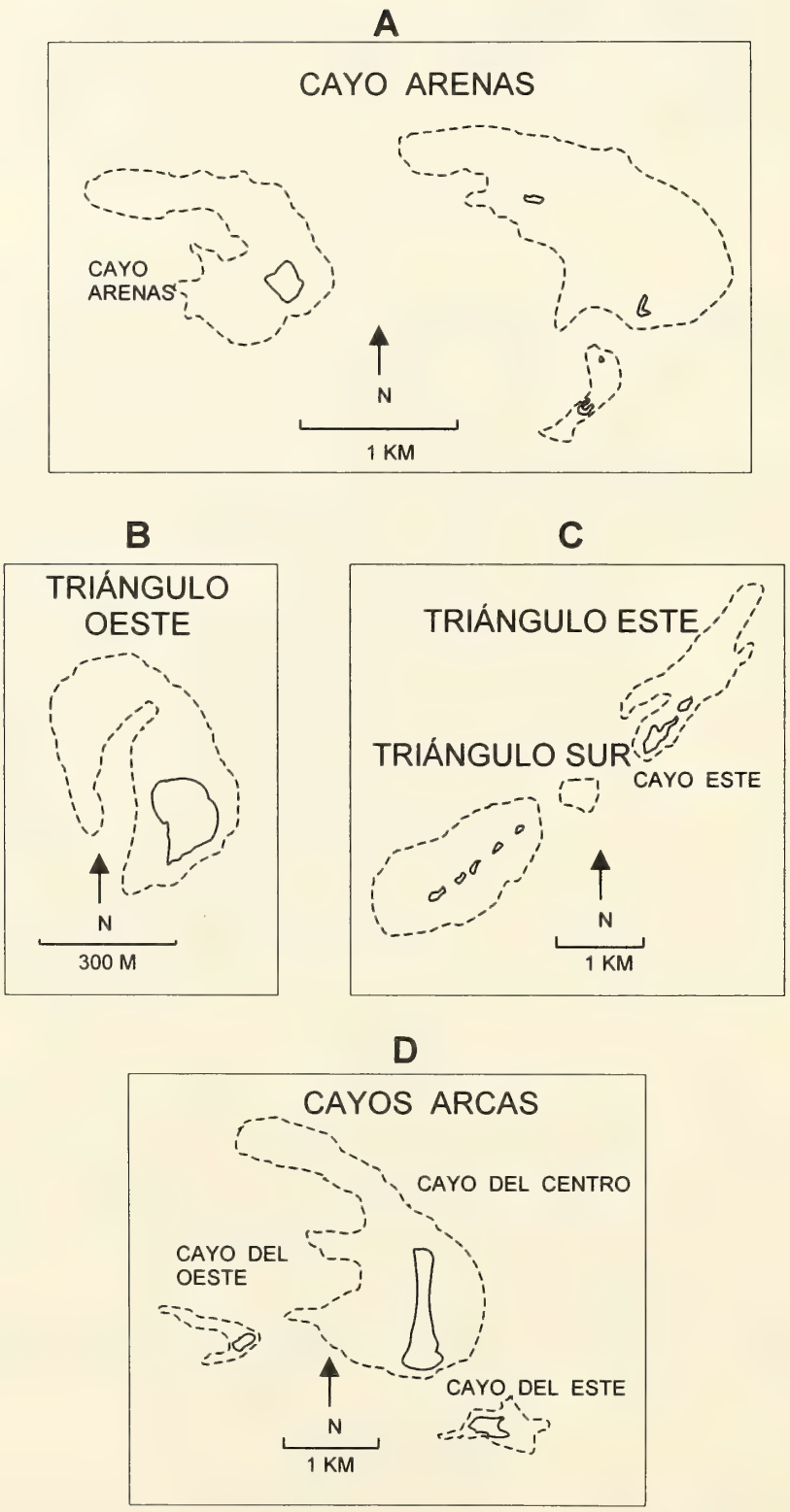

Figure 3. Maps of selected reef islands on Campeche Bank: A) Cayo Arenas; B) Triángulo Oeste; C) Triángulos Este and Sur; D) Cayos Arcas.

approximately 8 km apart (Figure 3B and C). The westernmost ridge has one emergent reef knoll, Triángulo Oeste, a small, sparsely vegetated island. Triángulo Oeste is composed primarily of coral rubble and has a lighthouse and several buildings that house a weather station and lighthouse keepers. The other ridge has several small, uninhabited islands located on two near-emergent reefs, Triángulo Este and Triángulo Sur, which are separated by approximately 800 m of water.

Cayos Arcas

Cayos Arcas is the southernmost reef-island complex on the Campeche Bank (Figure 3D), and it is also the most impacted by human activity (Tunnell 1992, Chávez and Tunnell 1993). Three reef masses, each with a low sandy cay, are emergent at Cayos Arcas (Logan 1969). Cayo del Centro is the largest island and has a manned lighthouse and weather station in addition to PEMEX buildings, tugboat mooring facilities, two helicopter pads, a volleyball court and a soccer field. A brief description of the vegetation on this island was provided by Paynter (1953) and Howell (1989). Cayo del Este, located approximately 1,500 m southeast of Cayo del Centro, is a small (140 m x 340 m), teardrop-shaped island. A proprietary PEMEX report listed seven species of plants that are found in a low, vegetated ridge that transverses the island. Cayo del Oeste, a diminutive (95 m x 130 m) island, having only a small, centrally located patch of vegetation, is located approximately 600 m west of the southernmost tip of Cayo del Centro.

METHODS

Initial access to the islands in the reef complexes of the Campeche Bank was aboard Mexican Navy vessels that disembarked from Progreso, Yucatán. A second trip to Arrecife Alacránes (July, 1986), was aboard a *Departamento de Pesca* vessel that departed from Yucalpeten, just east of Progreso. The islands of Arrecife Alacránes were visited during two periods from 20-31 January 1986 and 4-14 July 1986. The islands of Cayo Arenas were visited from 16-23 March, Arrecife Triángulos from 6-7 May, and Cayo Arcas from 20-26 April 1986. Surveys at the islands included camping on the islands, staying in lighthouse facilities at Alacrán, Arenas, and Arcas, and living aboard ship but making daily visits at Triángulo Oeste.

Complete counts of all nests on each island were made by dividing the island into sections, usually by vegetation type. However, the complexity of the vegetation and the close placement of nests made this technique impractical on Isla Perez and Isla Desertora, Arrecife Alacránes. Strip transects were used to estimate Brown Noddy (*Anous stolidus*) nests in 1.5-2.0 m-high *Suriana maritima* bushes on Isla Perez. A panoramic series of photographs were taken of the Masked Booby (*Sula dactylatra*) colonies on Isla Desertora and the photographic prints were overlapped in the laboratory to form total views of the colony areas. Counts of the birds on nests visible in each panorama were made to estimate the number of nests in each nesting area. Care was taken to identify situations where two adult birds might be present at a single nest and correct the nest count accordingly. We attempted to underestimate, rather than overestimate, the number of nests on each island.

In addition to counting or estimating nests, we also collected data on clutch size, the distance between nearest nests within colonies, and the ratio of occupied to empty nests on most islands. All avian censuses were conducted during the early morning or late evening hours to minimize disturbance to the birds and to avoid overheating of eggs or young.

RESULTS

Eight of the 12 permanently emergent Campeche Bank islands had active seabird nesting colonies during the study period. Nine species of colonial seabirds nested on the islands: Masked Booby; Brown Booby (*Sula leucogaster*); Red-footed Booby (*Sula sula*); Magnificent Frigatebird (*Fregata magnificens*); Laughing Gull (*Larus atricilla*); Royal Tern (*Sterna maxima*); Sandwich Tern (*Sterna sandvicensis*); Sooty Tern (*Sterna fuscata*); and Brown Noddy. Descriptions of colony locations in relation to vegetation or other island features and the results of bird censuses on each island are presented in the island accounts. Information on total numbers, habitat use, and breeding status of each species is provided in the species accounts.

Island Accounts

Arrecife Alacránes

Arrecife Alacránes was the only reef-island complex that was visited twice during the study. All five islands of this reef were sites of seabird nesting activity. The vegetation of the four most southerly islands was identified and mapped in 1899 by Millspaugh (1916), but Bonet and Rzedowski (1962) observed that the plant communities had changed considerably by the time of their survey in 1961. We found that additional changes in the species composition and distribution of vegetation had occurred in the intervening quarter of a century.

Isla Perez – The largest and most complex cay on the Alacrán platform, Isla Perez, was shaped like a shallow cresent with the long axis oriented towards the northeast (Figure 4). The island was flat with an average elevation of 1.3 m, but it had an elongate ridge that reached nearly 3.0 m in height just inland from the eastern shoreline. Bonet and Rzedowski (1962) listed 13 species of plants from Isla Perez. *Surina maritima* still covered most of the southern and northeastern ends of the island. The number of *Casuarina equisetifolia* (introduced Australian pine) increased since Bonet and Rzedowski's (1962) survey. The species was still common around the buildings and lighthouse in the central part of the island, but it had extended its distribution both northward and southward. The lee (west) side of the island was characterized by a broad, carbonate sand beach that fronted a low set of sand dunes dominated by *Tournefortia gnaphalodes*. A mixed grass-herbaceous community dominated by *Cenchrus* spp. occupied the strip between the dunes and the *S. maritima* stand. The *Opuntia dillenii* colonies had greatly expanded in size, but the small southwestern lagoon and mangroves had disappeared. A small pond encircled by *Avicennia germinans,* and not mentioned by Bonet and Rzedowski (1962), was found on the southeastern tip of the island. Two *Rhizophora mangle* plants also were found on the edge of the pond; this species was not reported previously on any Campeche Bank island.

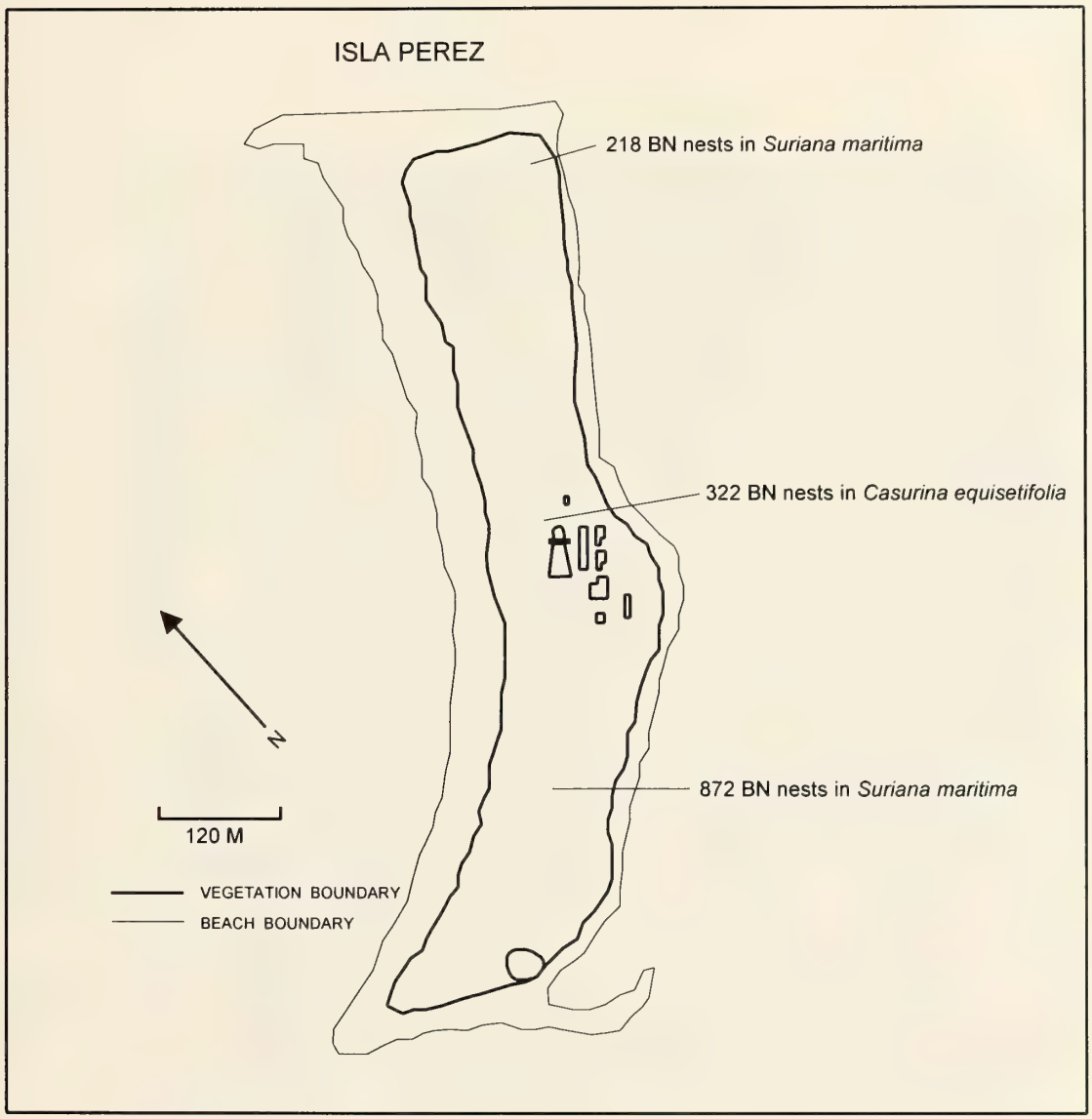

Figure 4. Schematic of Isla Perez, southwestern Alacrán Reef platform, showing Brown Noddy (BN) nesting locations.

No seabirds were nesting on Isla Perez when the island was visited in January. However, large colonies of Sooty Tern and Brown Noddy were active in July. The Sooty Tern colony occupied the northern portion of the island. Nests were scattered in barren areas within the *T. gnaphalodes* and *Cenchrus* spp. communities and beneath the *S. maritima* bushes. The Brown Noddy colony was located in the central and southern parts of the island. Nests were constructed in the branches of *S. maritima* and *C. equisetifolia*.

The Sooty Tern colony (Figure 5) was censused on 11 July 1986. It was impossible to obtain an accurate count of nests because the young birds had abandoned many nests to

Figure 5. View to south of Sooty Tern over *Cenchrus* spp. vegetation on northwestern corner of Isla Perez, Alácran Reef, 7 July 1986.

seek shade under the low bushes and trees. Consequently, we attempted to count the number of adult and juvenile birds in each vegetative community. Our counts were fairly accurate in the more open habitats, but we experienced difficulty in making counts of the immature birds in the *S. martima* areas. Immature birds in this area continuously scrambled about below the bushes. We counted a total of 26,160 Sooty Terns on the island. Of these, 13,570 were adult birds and 12,590 were juveniles. No Sooty Tern eggs were found during this survey. Approximately 75% of the terns were concentrated in the northernmost 150 m of the island, the area farthest removed from the buildings.

The Brown Noddy colony on the southern part of Isla Perez was censused on 7 July 1986. Nine transects running perpendicular to the axis of the island were censused by four people walking abreast. We counted 872 nests, but 555 were empty, 283 contained chicks and 34 had one egg each. Approximately 90% of the empty nests appeared to have been used for nesting and recently abandoned; the remainder looked as if they had not been used recently. Most of the nests were constructed in *S. maritima* and were from 0.15-1.5 m above the ground (Figure 6). The remainder of the nests in *C. equisetifolia* were situated 0.6-6.1 m above ground. The nests were constructed of sticks and most contained broken pieces of mollusk shells, most commonly the shells of an abundant lagoonal bivalve, *Codakia orbicularis*.

Within the central portion of the island, Brown Noddy nested only in *C. equisetifolia* trees. As many as 20 nests were found in a single tree and up to eight nests were placed on a single tree branch. We counted 322 nests in this area and most nests contained incubating or brooding adults. Egg and chick counts were not possible because most nests were constructed several meters above the ground.

Approximately 218 Brown Noddy nests also were located in *S. maritima* bushes in the middle of the Sooty Tern colony on the northeastern end of the island. Consequently, a total of 1,412 Brown Noddy nests on Isla Perez were counted in the three areas (see Figure 4). We believe that at least 1,357 of these nests were active during the preceding six months.

Isla Pájaros – The dimensions of Isla Parajos were estimated to be 183 m x 655 m in 1960 (Folk 1967), but we found the elevated, vegetated portion to be only half of the indicated length. The southern part of the island and mangrove lagoon that was described by Folk existed in 1986 only as a barren coral rubble spit. The remaining island was triangular with the spit extending southward. The central part of the island was lower than the periphery and existed as a flat sand plateau that was 1.0-1.5 m above sea level and covered with low vegetation. Bonet and Rzedowski (1962) listed 11 species of plants on the island. *Sporobolus virginicus* occurred around the periphery of the plant community and *Sesuvium portulacastrum* occupied the center. A few *S. maritima* and *T. gnaphalodes* bushes were scattered on the north and west sides of the island.

Only three nesting pairs of Masked Booby were found on the island in January. Each nest contained a single egg. Three active Masked Booby nests were observed in July. One nest contained a large downy chick and the other two nests held juveniles that were almost

Figure 6. Brown Noddy on nest filled with broken bivalve shells in *Suriana maritima* bush on south end of Isla Perez, Alácran Reef, 6 July 1986.

mature enough to fly. During both survey periods, the nests were located in barren sites among the *S. portulacastrum* plants in the center of the island.

Isla Chica – Located north of Isla Pájaros and across a narrow, deep-water passage, Isla Chica, the smallest of the Alacrán islands, was estimated to be 122 m wide by 198 m long in 1960 (Folk 1967), but appeared to be 70 m x 150 m in 1986. The island was shaped like an acute triangle with the acute apex pointed toward the southwest. The island was flat except for a slightly raised rim. There was a central grassy flat that was dominated by *S. virginicus* but with some patches of *S. portulacastrum*. A few low shrubs of *S. maritima* and *T. gnaphalodes* were present on the northeastern side of the island.

Although 18 Magnificent Frigatebirds were seen loafing on Isla Chica in January, no nesting birds were observed during that visit. Three species, Laughing Gull, Royal Tern, and Sandwich Tern, were nesting when the July visit was made. All nests were situated along a sandy berm on the northeastern margin of the island (Figure 7). The Sandwich Terns nested in two subcolonies. One subcolony occupied an area that was about 5 m in diameter and contained 43 nests. Eight of these nests contained newly hatched chicks. The remainder of the nests contained single eggs. The other Sandwich Tern subcolony contained 108 nests, but many of these nests were occupied by chicks that were mobile.

Royal Tern numbers were estimated from the number of chicks present because the nests were placed close to the vegetation and were difficult to see. Twenty-eight chicks were counted. Three Laughing Gull nests also were found in the vegetation near the tern nests.

Isla Desertora – Like Isla Pájaros and Isla Chica, Isla Desertora also appeared to be smaller than Folk (1967) described. The island retained its triangular outline, but was shorter and broader, measuring approximately 300 m x 700 m. A wide sandy beach encircled the island in front of a 1.5-2.0 m-high berm. The central portion of the island behind the berm was sparsely vegetated with a variety of species including *Cenchrus* spp., which was probably the most common plant. There were widely scattered, but locally dense, patches of *S. portulacastrum, S. virginicus, Tribulus alacranensis, Cakile edentula, Portulaca oleracea, Chamaesyce buxifolia,* and *O. dillenii.* The sandy berm along the northern edge and in the southwestern corner of the island was occupied by stands of *T. gnaphalodes.* A few *S. maritima* also were scattered in the southwestern part of the island.

The largest nesting concentrations of Masked Booby and Magnificent Frigatebirds on all the Campeche Bank islands existed on Isla Desertora. There were twice as many active nests of Masked Booby and six times more active nests of Magnificent Frigatebirds in January than there were in July. Red-footed Booby also were nesting on the island during both survey visits (Tunnell and Chapman 1988).

The main concentrations of Masked Booby nests in January were in the barren to sparsely vegetated areas on the northwestern and north-central sides of the island (Figure 8). A few nests also were scattered in open areas throughout the island. Within the areas having dense aggregations of nests, the nests contained large downy young or pre-flight juveniles. The nests in peripheral locations, however, mostly contained single eggs. Only one nest with

Figure 7. View to north over nesting colony of Royal and Sandwich terns and Laughing Gull on eastern end of Isla Chica, Alácran Reef, 7 July 1986.

Figure 8. View to northwest over Masked Booby nesting colony in central Isla Desertora, Alácran Reef, 28 January 1986.

two eggs was observed. Based upon an analysis of panoramic photographs of the island taken on 28 and 29 January, we estimated that 2,533 Masked Booby nests were present on the island.

In July, the Masked Booby nests were concentrated in two areas. The north-central subcolony had approximately 750 nests. This estimate was made by attempting to count nests from a location about 20 m from the periphery of the subcolony; the subcolony area was not entered because the daytime temperatures were too high. The nests in this area all contained eggs. The second subcolony was located in a sparsely vegetated region on the southwestern end of the island. This subcolony contained approximately 225 nests. Some nests in this area contained eggs, but there were nests with young in all stages of development. About 75% of the nests with eggs contained two eggs. About 50 additional Masked Booby nests were scattered about the island. Some of these nests were occupied by pairs of birds that were engaged in courtship rituals.

The Magnificent Frigatebird nests were located exclusively in thickets of *T. gnaphalodes* bushes (Figure 9). In January, there were seven distinct subcolonies of frigatebird nests on bushes just inland from the northeastern berm and three subcolonies near the southwestern corner of the island. A total of 163 nests were found in the northeastern subcolonies and 43 were counted in the southwestern subcolonies. Most of the nests contained eggs, but a few held small downy chicks. Many of the bushes supporting the nests appeared to be dead. When the July visit was made, frigatebird nesting activity appeared to be near the end of a cycle. Only 33 active nests were found, 31 in the northeastern area and two in the southwestern corner. All of the nests but one were occupied by large chicks. One nest, however, held two freshly hatched, naked chicks.

The Red-footed Booby nests also were situated in *T. gnaphalodes* bushes (Figure 10). Two active nests were found in January and one nest was found in July (Tunnell and Chapman 1988). Each nest contained a single egg.

Although no other seabirds were nesting during the January visits to Isla Desertora, small flocks of Sooty Tern and Laughing Gull harassed us when we were near the southeastern portion of the island in July. We found 10 juvenile Laughing Gull and 10 juvenile Sooty Tern hiding under vegetation (*S. maritima*) so dense that we may have missed other chicks. Brown Pelican (*Pelecanus occidentalis*) and immature Brown Booby were resting on the northwestern shore of the island during the January visit.

Isla Desterrada – Formed from the union of two islands, East and West Desterrada (Folk 1967), Isla Desterrada was over 2,000 m long. Vegetated portions occupied what was once the centers of the two islands at either end. Low sand dunes existed on the northern shores of the two vegetated areas. *Tournefortia gnaphalodes* was found in patches on and just behind the dunes, but the central portions of each vegetated area were composed of low-growing plants. The plant association consisted of *C. edentula, C. buxifolia, P. oleracea, Cenchrus* spp., and *T. alacranensis.* An automated light was present on the western end of the island but the light was turned over onto its side and was not functional. A concrete

Figure 9. View to northeast over Magnificent Frigatebird nesting in *Tournefortia gnaphalodes* adjacent to low dunes and beach on north side of Isla Desertora, Alácran Reef, 9 July 1986.

Figure 10. Red-footed Booby nesting in *Tournefortia gnaphalodes* in north-central portion of Isla Desertora, Alácran Reef, 9 July 1986.

platform, apparently a base to an old light, stood about 150 m offshore of the eastern end of the island and was extensively used as a seabird loafing perch.

We observed no nesting activity on the western end of island in January. During July, we found 50 juvenile Laughing Gull either walking or flying about the western end of Isla Desterrada. Because the walking young appeared unable to fly, we concluded that the western part of the island served as a colony site for the gulls but we could find no nests. Approximately 400 adult Laughing Gull circled the island or rested on its beaches during the visit.

Brown Booby and Magnificent Frigatebird were nesting on the eastern end of Isla Desterrada in January. Ten active Brown Booby nests were found on sandy substrates within the sparsely vegetated area, but it appeared that many more Brown Booby had just completed their nesting activities. Five of the nests contained eggs (three with one egg; two with two eggs), and the other nests held chicks. Approximately 200 Brown Booby were seen on the eastern end of the island and about 35% of those were immature birds.

We counted 52 Magnificent Frigatebird nests in low *T. gnaphalodes* bushes. Only 17 of the nests contained eggs and the remainder were empty. However, approximately 750 frigatebirds were seen flying above the island in a large "kettle" as we approached in both January and July.

The eastern end of Isla Desterrada had no active nests during the July visit. However, 65 adult Brown Booby, two Brown Pelican, two Black Skimmer (*Rynchops niger*), and approximately 30 Royal Tern, 30 Sandwich Tern and 40 Laughing Gull were loafing on the beach.

Cayo Arenas

Three small, unnamed, barren islands showed no sign that they were used as nest sites. Only the largest vegetated island, Cayo Arenas, contained an active colony of nesting Masked Booby. A strong "*norte*" causing rough seas confined investigators to the island for several days and consequently allowed the booby colony to be thoroughly surveyed.

Situated on the leeward reef platform, Cayo Arenas had a maximum elevation of 3 m and measured 240 m x 275 m at its widest points. A lighthouse was centrally located on the island (Figure 11). Calcareous sand formed most of the island substrate, but coral boulders were distributed along the eastern side. Large "thickets" of *T. gnaphalodes* occupied the dunes on the west side and the entire northern quarter of the island. Colonies of *O. dillenii* were distributed throughout the southern end of the island and the cactus appeared to be expanding and choking out the *T. gnaphalodes* in some locations. The cactus also occurred in a smaller area of the southwestern island corner. Low vegetation, including *Ipomoea pes-caprae, P. oleracea, and Cenchrus* spp., were found in zones surrounding the lighthouse area. The lighthouse was also surrounded by introduced vegetation such as *C. equisitifolia, Cocos nucifera* (coconut palm), *Crinum americanum* (spider lily), and *Cordia dodecandra* (siricote).

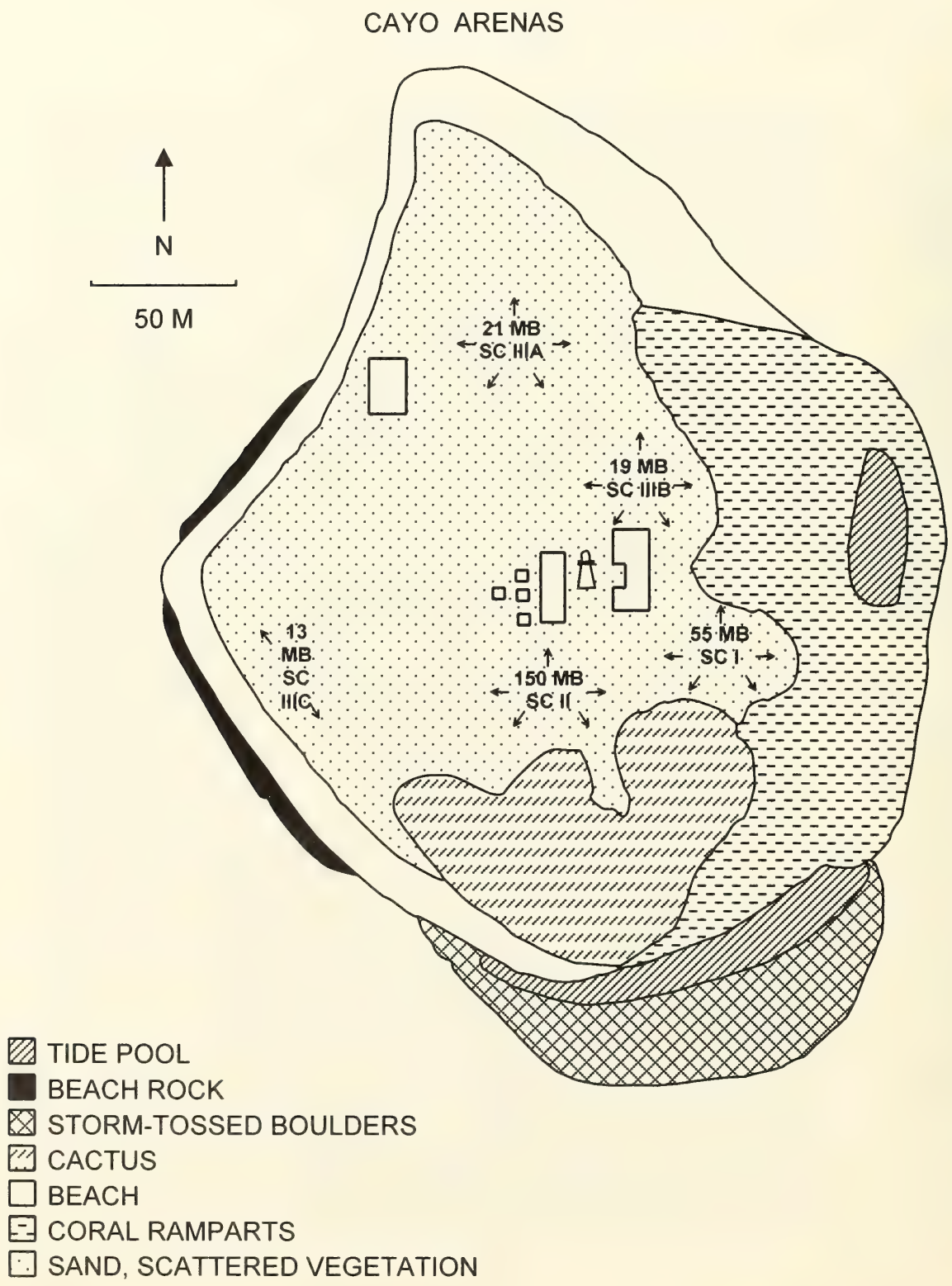

Figure 11. Cayo Arenas showing distribution of substrate types and location and number of nests in three Masked Booby subcolonies (I, II, III A, B, C).

Three Masked Booby subcolonies were evident. Subcolony I was located to the southeast of the lighthouse on the east-central part of the island and contained 55 nests. The nests were located in areas of bare sand interspersed among patches of *P. oleracea*, scattered coral rubble, and boulders. The colony area was bounded to the north by a coral boulder field and to the south by a stand of *O. dillenii*. The birds in this subcolony must have been the first to initiate nesting because most of the young were nearly ready for flight. A few nests, however, contained eggs or downy chicks.

Subcolony II, containing 150 nests, was located in a large, sandy, barren area south of the lighthouse (Figure 12). It was protected from prevailing winds by the lighthouse and the associated buildings to the north, dense colonies of *O. dillenii* to the east and southwest, and a hedge of *T. gnaphalodes* to the west. The nests contained eggs or chicks, but none of the chicks were over 20 days old. Average distances between nearest nests were determined for two sets of 20 adjacent nests in this subcolony. One set of nests was centrally located in a barren sandy area and the other set was in an area where *P. oleracea* grew between the "scrape" nests. Inter-nest distances were greater in the *P. oleracea* area. Mean inter-nest distance was 2.9 m (s = 1.08) where vegetation was present but was only 1.6 m (s = 0.42) when nests were in bare sand.

The third subcolony, located on the periphery of the island, was loosely defined. The nests in this subcolony were scattered through several low-growing vegetative associations or areas of bare sand. All 53 nests in this subcolony contained eggs.

A total of 258 active Masked Booby nests were counted on Cayo Arenas (Figure 13). We found an additional 17 abandoned nests that contained eggs in a bare sandy area between subcolonies I and II. A domestic cat and dog were kept as pets on the island and these animals may have been responsible for some egg and chick loss or nest abandonment. The dog, which on two occasions was observed returning to the lighthouse from the area of subcolony III, appeared to have severe puncture wounds all over his head, especially around his eyes and nose.

The coral boulder area on the northeastern margin of the island was used as both a daytime loafing area and a night roost by the boobies. Up to 300 birds congregated in the area at night. Other birds observed on or near Cayo Arenas included 15 Magnificent Frigatebird, an Osprey (*Pandion haliaetus*), 7 Great Blue Heron (*Ardea herodias*), 3 Great Egret (*Ardea alba*), 2 Tricolored Heron (*Egretta tricolor*), 7 Cattle Egret (*Bubulcus ibis*), a Black-crowned Night-Heron (*Nycticorax nycticorax*), 13 Ruddy Turnstone (*Arenaria interpres*), 3 Laughing Gull, 47 Royal Tern, 3 Sandwich Tern, 2 Yellow-rumped (Myrtle race) Warbler (*Dendroica coronata*), a Barn Swallow (*Hirundo rustica*), and many small shorebirds.

Arrecifes Triángulos

An emergency sea-rescue operation diverted the ship before Triángulos Este or Sur could be visited. Triángulo Oeste was surveyed, however.

Figure 12. View to northwest of Masked Booby Subcolony II on Cayo Arenas, 17 March 1986.

Figure 13. Masked Booby nesting pair and chick on Cayo Arenas, 17 March 1986.

Triángulo Oeste – The only vegetation on Triángulo Oeste is a row of *T. gnaphalodes* that stretched eastward from the lighthouse, some scattered *C. buxifolia*, a single *S. maritima*, and one *C. nucifera*. No nesting activity was observed on this small coral rubble island.

Magnificent Frigatebird were the only seabirds seen in the area and they were riding the up-drafts next to, and over, the lighthouse and associated dwellings.

Triángulos Este and Sur – The lighthouse keeper on Triángulo Oeste reported that "*gaviotas*" nested on Triángulos Este and Sur. Unfortunately, "*gaviota*", which is Spanish for "gull" or "tern", is a generic term used by the local fishermen to include most species of seabirds. The presence of many gulls, terns and boobies roosting on or circling the islands was confirmed with binoculars from the ship's deck. However, we could not determine whether or not nesting was taking place.

Cayos Arcas

Cayos Arcas has become an offshore staging area for a rapidly developing oilfield on the surrounding continental shelf. An offshore platform terminal, two floating oil loading terminals, and two oil tankers were visible from Cayo Centro during the bird census. Closer to shore, and within the natural protection of the leeward lagoon, 6-15 tugboats and oilfield service boats always were present. Oilfield debris was observed on the islands and surrounding reefs. Despite this level of human activity, two of the three islands in this reef-island complex had active colonies of Masked Booby and Magnificent Frigatebird.

Cayo del Centro – The largest of the islands in the Cayos Arcas complex, Cayo del Centro was approximately 850m long and oriented in a north-south direction (Figure 14). It was somewhat broader at the north end (300 m) than at the south end. A sandy beach encircled the island, but there were a few areas of coral rubble and tidal pools along the narrow eastern shore. The vegetation was predominately low ground cover. *Cenchrus* spp. and *S. portulacastrum* were the most common components of the ground cover, but the eastern beach ridge had scattered patches of *T. gnaphalodes* and *Scaevola plumieri* bushes. A small *A. germinans* swamp surrounded by *Batis maritima* was located on the southwestern edge of the island. Around the lighthouse and other buildings, there were several introduced species including *C. equisetifolia* and one *C. nucifera*.

Masked Booby nesting on Cayo del Centro were segregated into five subcolonies. Two subcolonies were situated on bare sand areas on the northwest and southwest margins of the island (Figure 15) and the other three were located within the low vegetation near the center of the island. We counted a total of 453 Masked Booby nests that contained eggs or young. An additional 203 immature booby chicks that had apparently left their nests also were counted. Based upon these counts, we estimated that the Masked Booby colony on Cayo del Centro contained in excess of 600 nests.

Magnificent Frigatebird also nested within distinct subcolonies on Cayo del Centro. All of the 15 subcolonies except one were located in clumps of elevated vegetation (Table 1). The highest densities of nests were located in *A. germinans* and atop *S. maritima* bushes.

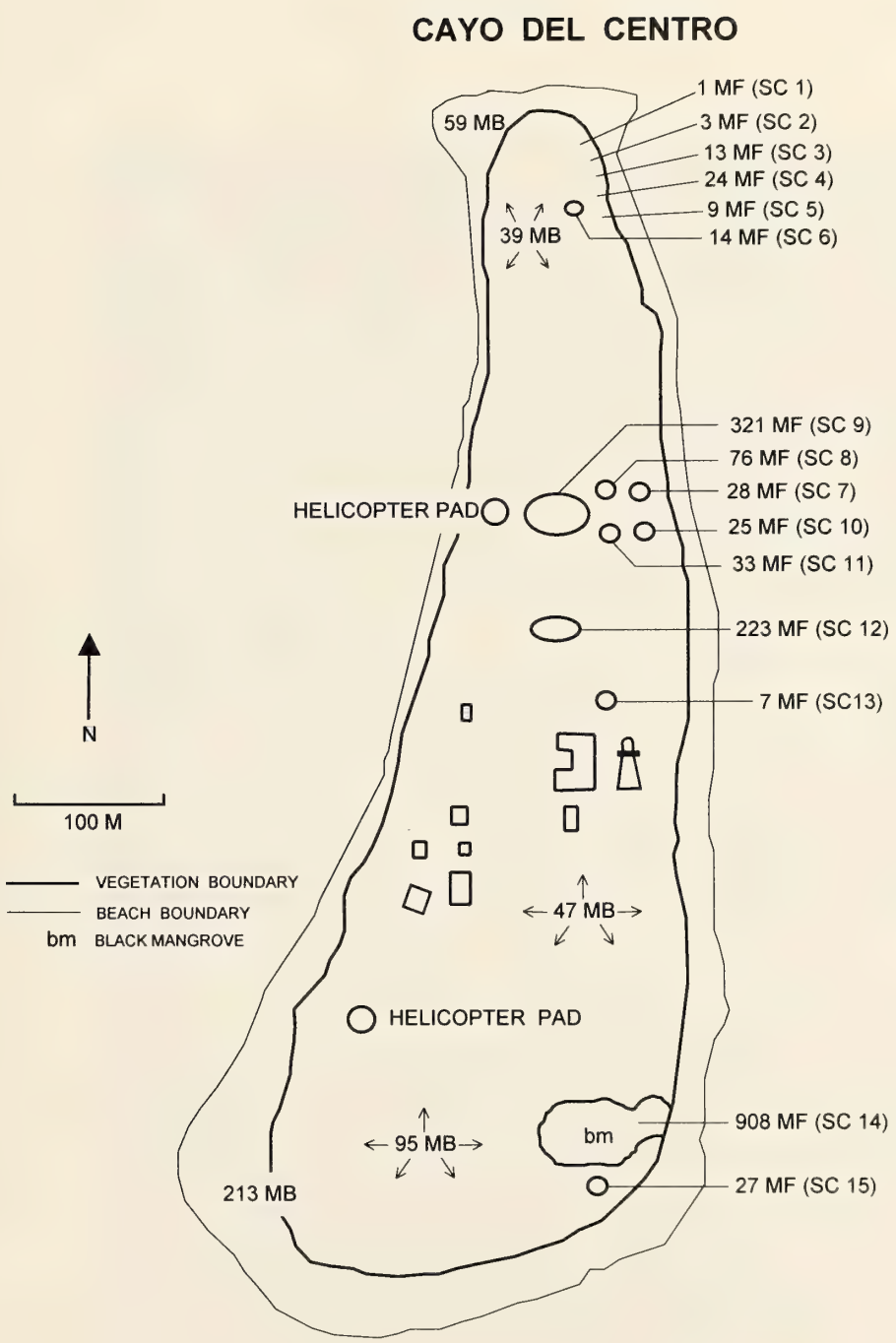

Figure 14. Cayo del Centro in Cayos Arcas reef group, showing Masked Booby (MB) and Magnificent Frigatebird (MF) subcolonies (SC), 21 April 1986.

Figure 15. View to northwest over Masked Booby nesting colony on upper beach berm, southwestern corner, Cayo del Centro, Cayos Arcas, 21 April 1986.

Table 1. Number of nests and chicks in the 15 different subcolonies of Magnificent Frigatebird on Cayo del Centro, Cayos Arcas, 21 April 1986.

Subcolony Number[1]	Number of Nests	Number of Chicks	Vegetation; Location
1	1	1	*T. gnaphalodes*; northeast dunes
2	3	2	*T. gnaphalodes*; northeast dunes
3	13	10	*T. gnaphalodes*; northeast dunes
4	24	25	*T. gnaphalodes*; northeast dunes
5	9	8	*T. gnaphalodes*; northeast dunes
6	14	13	*S. maritima*; inland from northeast dunes
7	28	24	*S. maritima*; northeast central
8	76	71	*S. maritima*; northeast central
9	321[2]	255	*S. maritima*; central, north
10	25	13	*S. maritima*; northeast central
11	33	13	*S. maritima*; northeast central
12	223	176	*S. maritima*; central, north
13	7	4	*S. maritima*; east, central
14	908[2]	720	*A. germinans*; southwest
15	27	23	*B. maritima*; southwest
TOTAL	1,712	1,358	

[1] Arranged from north to south.

[2] Nests counts for subcolonies 9 and 14 were calculated by an average ratio of other subcolony nests to chicks, since densities were so high and nests were so close together, counting in the field proved impossible.

One subcolony was composed of nests placed on the ground within dense thickets of *B. maritima.* Almost all of the elevated nesting habitats preferred by the frigatebirds appeared to be utilized. In some subcolonies, the nests were less than 0.3 m apart and the guano deposits appeared to be killing the bushes. In others, the nests were built atop mounds of guano that were 0.5 m high (Figure 16). We counted 1,712 nests and all of the nests contained chicks.

Cayo del Este – The vegetation on this island was low and consisted predominantly of *Cenchrus* spp. and *S. portulacastrum.* Several clumps of dead *T. gnaphalodes* and *S. maritima* bushes also were scattered about the island (Figure 17). Only two species of birds, Masked Booby and Magnificent Frigatebird, were nesting on Cayo del Este, but Sooty Tern, Royal Tern, Sandwich Tern and Laughing Gull were common around the island.

Masked Booby nested within two subcolonies. One subcolony, located on the eastern end of the island, contained 58 nests. All of these nests held eggs except for two that contained chicks. The other subcolony, comprised of 40 nests with either eggs or chicks in various stages of development, was established on the western end of the island.

Figure 16. View to southeast of immature Magnificent Frigatebirds in nesting colony on dead or dying *Tournefortia gnaphalodes* bushes, north-central Cayo del Centro, Cayos Arcas, 21 April 1986.

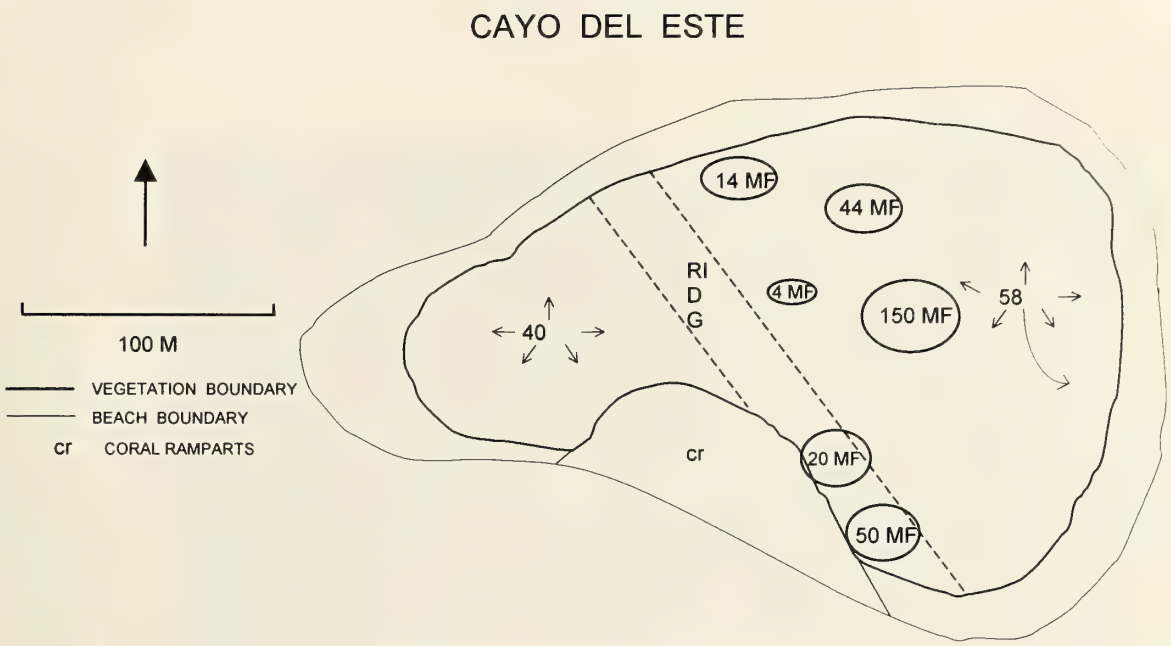

Figure 17. Cayo del Este in Cayos Arcas reef group showing Masked Booby (MB) and Magnificent Frigatebird (MF) subcolonies, 21 April 1986.

Magnificent Frigatebird nested in six subcolonies on Cayo del Este. The largest subcolony, located near the center of the island, was situated in a barren area where the nests were constructed on the ground or on small mounds of guano (Figure 18). Many of the nests appeared abandoned. The remainder of the subcolonies were positioned in clumps of *T. gnaphalodes* or *S. maritima* bushes. Most of the bushes in these clumps were dead. There was a total of 282 nests which contained 198 chicks in the six subcolonies. We found no eggs and all of the chicks were large but unable to fly.

Cayo del Oeste – There was no nesting activity on Cayo del Oeste when the island was visited late in the afternoon of 22 April. The small central patch of vegetation contained only two *S. maritima* bushes and these bushes were used as resting or roosting sites by frigatebirds.

Species Accounts

The stage in the breeding cycle is one of the most important factors in determining the accuracy of population estimates in colonially nesting seabirds (Nelson 1979, Duffy and Nettleship 1992). In more equatorial regions some individuals of certain species breed during every month (Nelson 1978) and the adults and young leave the colonies when the young fledge. The constant turnover of breeding pairs at a site complicates the census of a seabird population.

Figure 18. View to northeast of immature Magnificent Frigatebirds in nesting colony of dead *Tournefortia gnaphalodes* surrounded by *Sesuvium portulacastrum*, Cayo del Este, Cayos Arcas, 21 April 1986.

Unfortunately, the annual breeding cycle of seabirds in the southern Gulf of México is poorly known and, consequently, we cannot be sure that our visits to the islands coincided with the peak of the breeding cycle. In the species accounts below we discuss the breeding status of the Campeche Bank seabirds and compare our notes to published information. English and scientific names in the species accounts, and the taxonomic sequence in which the species are listed, follow the American Ornithologists Union Checklist (A.O.U. 1998). The species accounts provide a complete historical summary of nesting records for each species on each island. We also comment on our survey results.

Masked Booby (*Sula dactalytra*)

Masked Booby are among the most abundant and widely distributed members of the Sulidae and are found throughout the pan-tropical blue water belt (Nelson 1978). A highly pelagic species that feed primarily on flying fish and squid (Murphy 1936, Anderson 1993), Masked Booby rarely feed inshore (Kepler 1969). Throughout their range, these boobies nest on small barren or poorly vegetated islands (Gillham 1977) in colonies that are relatively small and of low density (Clapp et al. 1982). As few as a single pair may nest on some islands (Dorward 1962) but several colonies with up to 2,500 pairs are known (Nelson 1967), and at least one colony may have as many as 15,000 pairs (Hutchinson 1950). Most colonies contain from 50 to several hundred pairs (Nelson 1978, Clapp et al. 1982). Because the colonies on the Campeche Bank islands have been inadequately described, van Halewyn and Norton (1984) concluded that the Masked Booby was the scarcest booby in the Caribbean.

Probably because of their size and conspicuousness, there are more historical records of Masked Booby nesting on the Campeche Bank islands than any other species (Table 2). At various times Masked Booby have been recorded nesting on all but four of the 12 islands in the four largest reef complexes. We found a combined total of 4,519 active nests on five of the islands and we provided the first record of a Masked Booby colony on Cayo del Este.

The period of peak nesting for Masked Booby on the Campeche Bank islands is not known. The inhabitants of Cayos Arcas told Paynter (1955) that the peak nesting season was in June and July and Clapp et al. (1982) concurred. Nelson (1978) suggested that Masked Booby in the Caribbean and Atlantic nested annually with the period of heaviest laying occurring between February and mid-August. A second season of an intermediate amount of laying may also occur from November to January (Nelson 1978). The historical record (Table 2) indicates that Masked Booby nesting activities have been observed in all months except December and February. Since we found many more active nests in January than we did in July on Isla Desertora and Boswall (1978) reported that 2,000 adults and young were present on Isla Desertora in September, the nesting cycle on the Campeche Bank islands may differ from those found elsewhere in the region. We suspect that some Masked Booby may be engaged in various stages of breeding activities throughout the year in the southern Gulf of México. Peaks in the breeding cycle and usage of some islands may be somewhat irregular as is common elsewhere among Masked Booby populations (Nelson 1978, Anderson 1993).

Table 2. Historical record and summary of seabird colonies on Campeche Bank reef islands (NC = no comment on colony status or size; "?" = date not mentioned).

Reef Group or Island	Species/Colony Size	Date	Source
Arrecife Alacrán	Boobies/"vast abundance"	1675	Dampier 1699
	Magnificent Frigatebird/NC	1675	Dampier 1699
	Egg-birds/(? = Sooty Terns)/NC	1675	Dampier 1699
	Boobies /"swarms"	?	Smith 1838
	Magnificent Frigatebird/NC	?	Smith 1838
	Sooty Tern/"nesting"	?	Lowery & Newman 1954
	Masked Booby/"nesting"	June 1959	Kornicker et al. 1959
	Brown Booby/"nesting"	June 1959	Kornicker et al. 1959
	Magnificent Frigatebird/"nesting"	June 1959	Kornicker et al. 1959
	Laughing Gull/"nesting"	June 1959	Kornicker et al. 1959
	Royal Tern/"nesting"	June 1959	Kornicker et al. 1959
	Sooty Tern/"nesting"	June 1959	Kornicker et al. 1959
	Brown Noddy/"nesting"	June 1959	Kornicker et al. 1959
Isla Perez	Sooty Tern/"carpeted with eggs in nesting season"	?	Paynter 1955
	Brown Noddy/"over 1,000 birds must breed on the island"	?	Paynter 1955
	Laughing Gull/"numerous" eggs	1955-61	Bonet & Rzedowski 1962
	Brown Noddy/"numerous" eggs	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/NC	1955-61	Bonet & Rzedowski 1962
	Sooty Tern/10s of 1,000's of birds	July 1961	Fosberg 1962
	Brown Noddy/many nests	July 1961	Fosberg 1962
	Magnificent Frigatebird/48 empty nests	Sept. 1975	Boswall 1978
	Brown Noddy/2,000 birds	Sept. 1975	Boswall 1978
	Royal Tern/800 birds	Oct. 1984	Howell 1989
	Sandwich Tern/250 birds	Oct. 1984	Howell 1989
	Laughing Gull/500 birds	Oct. 1984	Howell 1989
	Sooty Tern/26,160 birds	July 1986	This paper
	Brown Noddy/1,357 nests	July 1986	This paper
	Sooty Terns/~20,000 birds	Apr. 1988	Lockwood 1989
	Brown Noddy/~2,000 nesting	Apr. 1988	Lockwood 1989
Isla Chica	Masked Booby/50 nests	May 1912	Kennedy 1917
	Masked & Brown Booby/6-8 pairs nesting	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/"nesting"	1955-61	Bonet & Rzedowski 1962
	Masked Bobby/8-10 nests	July 1961	Fosberg 1962
	Laughing Gull/3 nests	July 1986	This paper
	Royal Tern/28 nests	July 1986	This paper
	Sandwich Tern/151 nests	July 1986	This paper

Table 2. Continued.

Reef Group or Island	Species/Colony Size	Date	Source
Isla Pájaros	Sooty Tern/"thousands"	May 1912	Kennedy 1917
	Sandwich Tern/50 nests	May 1912	Kennedy 1917
	Masked Booby/1 nest	May 1912	Kennedy 1917
	Laughing Gull/4 nests	May 1912	Kennedy 1917
	Masked Booby/200 birds	Sept. 1952	Paynter 1955
	Brown Booby/500 birds (nesting reported)	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/numerous	Oct. 1952	Siebenaler 1954
	Brown Booby/NC	Oct. 1952	Siebenaler 1954
	Brown & Masked Booby/"nesting"	1955-61	Bonet & Rzedowski 1962
	Magnificent Frigatebird/"nesting"	1955-61	Bonet & Rzedowski 1962
	Masked Booby/100+ nests	July 1962	Fosberg 1962
	Masked Booby/3 nests	Jan. & July 1986	This paper
	Masked Booby/"a few nesting"	Apr. 1988	Lockwood 1989
Isla Desertora	Magnificent Frigatebird/NC	1899	Millspaugh 1916
	Masked Booby/NC	1899	Millspaugh 1916
	Masked & Brown Booby/"nesting"	1955-61	Bonet & Rzedowski 1962
	Masked Booby/100s "nesting"	July 1961	Fosberg 1962
	Magnificent Frigatebird/"many" nesting	July 1961	Fosberg 1962
	Masked Booby/2,000 nests	Sept. 1975	Boswall 1978
	Magnificent Frigatebird/2,000-3,000 birds	Oct. 1984	Howell 1989
	Red-footed Booby/2 nests	Jan. 1986	Tunnell & Chapman 1988
	Masked Booby/2,533 nests	Jan. 1986	This paper
	Magnificent Frigatebird/206 nests	Jan. 1986	This paper
	Red-footed Booby/1 nest	July 1986	Tunnell & Chapman 1988
	Masked Booby 1,025 nests	July 1986	This paper
	Magnificent Frigatebird/33 nests	July 1986	This paper
	Laughing Gull/10 nests	July 1986	This paper
	Sooty Tern/10 nests	July 1986	This paper
	Magnificent Frigatebird/"nesting"	Apr. 1988	Lockwood 1989
	Masked Booby/"nesting"	Apr. 1988	Lockwood 1989
	Red-footed Booby/1 nest	Apr. 1988	Lockwood 1989
Isla Desterrada	Brown Booby/300 birds (nesting reported)	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/"many nests"	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/2,500 nests	Oct. 1952	Paynter 1955
	Boobies/"nesting"	1955-61	Bonet & Rzedowski 1962

Table 2. Continued.

Reef Group or Island	Species/Colony Size	Date	Source
	Royal Tern/nesting (?)	July 1961	Fosberg 1962
	Brown Booby/10 nests	Jan. 1986	This paper
	Magnificent Frigatebird/52 nests	Jan. 1986	This paper
	Laughing Gull/50 nests	July 1986	This paper
	Brown Booby/"nesting" (small colony)	Apr. 1988	Lockwood 1989
Cayo Arenas	Masked Booby/400 birds	Sept. 1952	Paynter 1955
	Masked Booby/500 pairs	Oct. 1984	Howell 1989
	Masked Booby/258 nests	Mar. 1986	This paper
3 Unnamed Islands	No vegetation or nesting reported		
Triangulos	Boobies/"plenty"	1675	Dampier 1699
	Magnificent Frigatebird/NC	1675	Dampier 1699
Triangulo Oeste	No official nesting records		
Triangulo Sur	No nesting records; fisherman & lighthouse keeper at Triangulo Oeste report nesting		
Triangulo Este	Masked Booby/"nesting"	1886(?)	Ward 1887
	Magnificent Frigatebird/"nesting"	1886(?)	Ward 1887
	Royal Tern/"observed"	1886(?)	Ward 1887
Cayos Arcas	Sooty Tern/"nesting"?	?	Lowery & Newman 1954
	Masked Booby/500 birds	Sept. 1952	Paynter 1955
	Magnificent Frigatebird/500 birds nesting	Aug. 1952	Paynter 1955
	Masked Booby/250 pairs (+2,000 birds)	Oct. 1984	Howell 1989
	Magnificent Frigatebird/~2,500 pairs	Oct. 1984	Howell 1989
Cayo del Centro	Masked Booby/600+ nests	Apr. 1986	This paper
	Magnificent Frigatebird/1,712 nests	Apr. 1986	This paper
Cayo del Este	Masked Booby/98 nests	Apr. 1986	This paper
	Magnificent Frigatebird/282 nests	Apr. 1986	This paper
Cayo del Oeste	No nesting recorded		

We found that the Masked Booby is much more abundant in the eastern Caribbean than formerly believed. If the IXTOC-I oil spill severely affected the population of Masked Booby in the southern Gulf of México (Duncan and Havard 1980), the species appears to have recovered. Based upon the summaries of known colonies listed in Nelson (1978), the colony on Isla Desertora is the largest nesting concentration of the species in the eastern Caribbean region. If the colonies on the Campeche Bank islands are considered as either a temporal or a geographical unit, the nesting concentration may rank among the largest in the world.

Brown Booby (*Sula leucogaster*)

The Brown Booby, which often nests in association with Masked and Red-footed boobies, may be the most common booby in the world (Nelson 1978). It breeds pantropically and occupies habitats that are similar to those of the Masked Booby (Dorward 1962), but the Brown Booby feeds closer to shore and can tolerate muddier water (Murphy 1936). The breeding ecology of the species was described by Chapman (1908), Thayer (1911), Dorward (1962), Simmons (1967) and Nelson (1978).

Despite Lowery and Newman's (1954) claim that the species did not breed on islands in the Gulf of México, Brown Booby colonies were reported from three islands on Arrecife Alacránes. Kornicker et al. (1959) listed the species as one of seven seabirds that they observed nesting on the Alacrán islands in June, 1959, but they did not indicate where they saw the birds or the stage of the nesting cycle. Paynter (1955) saw 300 birds on Isla Pájaros in early September 1952, but the birds were not nesting at the time. Bonet and Rzedowski (1962) however, photographed a pair of Brown Booby on the nest sometime during their visits to Isla Pájaros in 1960 or 1961. They also photographically documented the nesting of Brown Booby on Isla Desertora. Neither Paynter (1955) nor Boswall (1978) saw Brown Booby nests on Isla Desterrada, but according to the lighthouse keeper on the island, the boobies nested there in the spring. Our visit to Isla Desterrada predated Lockwood's (1989) by almost a year, and we also found a small colony of Brown Booby. Lockwood's account does not mention the stage of nesting that he observed in April, but we found that most of the young had fledged in January and we saw no signs of nesting activity in July. Boswall (1978) found no signs of nesting activity when he visited Isla Desertora in mid-September.

Although Nelson (1978) indicates that the period of heaviest laying in the Caribbean and Atlantic occurs from October to May and a limited amount of egg laying may occur during the remainder of the year, we feel that the breeding season for Brown Booby is much more restricted in the southern Gulf. The heaviest period of laying probably occurs from October to March. Some laying activity may also occur from April through June but there appears to be no nesting activity during the rest of the year. We found no evidence in historical accounts to justify the assumption by Friedmann et al. (1950) that Brown Booby nested on Cayos Arcas. Although the habitats on Cayo del Centro appear suitable, we did not find any indication that Brown Booby nested there recently. Since the Brown Booby is the least pelagic booby, van Halewyn and Norton (1984) suggested the species might be more vulnerable to oil spills. If the species nested on Cayos Arcas in the past, contamination

from the IXTOC-I oil spill may have affected the population. Cayos Arcas is the reef complex that is located closest to the site of the IXTOC-I well blowout.

Red-footed Booby (*Sula sula*)

Although the Red-footed Booby is distributed pantropically (Nelson 1978, Schreiber et al. 1996) and is among the world's most abundant boobies, it has rarely been observed in the Gulf of México (Lowery and Newman 1954, Clapp et al. 1982). It had not been recorded nesting in the Gulf until Tunnell and Chapman (1988) reported active nests in January and July on Isla Desertora, Alacrán reef. The following year, Lockwood (1989) again found an active nest on the same island during an April visit. Since the nearest known colony of Red-footed Booby was at Half Moon Cay, Belize (Verner 1961), approximately 600 km away, this represented a significant extension of the breeding range of the species.

Since the Red-footed Booby is one of only two sulid species that regularly nest in shrubs or low trees (Nelson 1969, Schreiber et al. 1996), its presence as a breeding bird is generally limited to islands with vegetation tall enough to support an elevated nest (Murphy 1936). The occurrence of low *T. gnaphalodes* bushes on Isla Desertora has been relatively recent. Millspaugh (1916) found no shrubby vegetation during his survey in 1899 and Bonet and Rzedowski (1962) and Fosberg (1962) found only a few scattered bushes some 60 years later. By the time of our visit, the *T. gnaphalodes* had developed substantially, forming hedge-like clumps.

According to Nelson (1978), the period of heaviest egg laying for the Red-footed Booby in the Atlantic and Caribbean is from August to March. Based on only three observation periods of a total of four nests, we cannot speculate about the breeding season for the species in the southern Gulf. However, the nesting season on Isla Desertora is probably from November to April as occurs on Half Moon Cay (Verner 1961) and Little Cayman Island (Diamond 1980).

Magnificent Frigatebird (*Fregata magnificens*)

The Magnificent Frigatebird, one of five species of the pantropically distributed Fregatidae (Nelson 1975), breeds on both coasts of México and Central America and the northern coasts of South America (A.O.U. 1998). Colonies in the Gulf of México have been reported from Laguna de Tamiahua, Veracruz (Lowery and Newman 1954), and the Marquesas Keys, Florida (Harrington et al. 1972). A single frigatebird nest containing eggs also was reported on the Texas coast (J. J. Carroll *in* Oberholser and Kincaid 1974).

Throughout their range, frigatebirds construct nests in shrubs or low trees on islands where there is a minimum of human disturbance (Chapman 1908, Eisenmann 1962). Because frigatebirds are adept at perching, they can nest in a wide range of habitats (Nelson 1975). Nests appear to be oriented to permit easy landing (Diamond 1973, 1975), but the spatial distribution of nests is not random or uniform. Frigatebirds nest in distinct clumps (Nelson 1975) and reported nest densities range from 1.3 nests/m^2 (Eisenmann 1962) to 0.28 nests/m^2 (Diamond 1973).

According to Diamond (1973), Magnificent Frigatebird on Barbuda have an egg-laying season that extends from September through January. An examination of the historical record of the Campeche Bank colonies indicates that the laying season in the southern Gulf is similar to that on Barbuda. Nest construction was initiated in August (Paynter 1955), but eggs were not seen in nests until September (Paynter 1955) or October (Howell 1989).

Colonies of Magnificent Frigatebird were primarily limited to those islands with sufficient shrubby vegetation to support nests. On Arrecife Alacránes only Isla Chica and Isla Pájaros were not used as nesting sites. These islands possessed a few low shrubs, but the woody plants were scattered and had not formed clumps of significant size for nesting. If more woody vegetation develops on these islands, Magnificent Frigatebird may nest there. The colony that we recorded on Cayo del Este, Cayos Arcas, represented the first record of Magnificent Frigatebird nesting on that island. There, many of them nest directly on the ground and not in the usual woody shrubs. Some nesting may eventually be seen on Cayo del Oeste as well because frigatebirds frequent the small clumps of *S. maritima* and *T. gnaphalodes* for roost sites.

Laughing Gull (*Larus atricilla*)

Colonies of nesting Laughing Gull are found primarily along the Atlantic and Gulf coasts of the United States, but they also breed in the Caribbean, on the northern coast of South America, and along the Pacific coast of southern México (A.O.U. 1998, Clapp et al. 1983, Burger 1996). The habitats chosen as nesting sites vary considerably throughout the range of the species and colony descriptions from nesting areas along the Atlantic and Gulf of México are summarized by Clapp et al. (1983). Nesting habits in the Caribbean and southern Gulf of México are less well known. Brief descriptions of Laughing Gull colonies from Caribbean locations are provided by Dewey and Nellis (1980) and Burger and Gochfield (1985).

The report of four nests of Laughing Gull on Arrecife Alacránes by van Halewyn and Norton (1984) was possibly based upon the account by Kennedy (1917) who reported four Laughing Gull nests on Isla Pájaros. Bonet and Rzedowski (1962: Fig. 11) included a photograph of a Laughing Gull colony on Isla Perez in their report on the vegetation of Alacrán and, based on a count of the visible nests, the colony contained a minimum of 100 pairs. Fosberg (1962) found 20-30 Laughing Gull on Isla Chica during his visit in July 1962, but was able to locate only a single nest with eggs.

We found no nesting Laughing Gull during our January visits to the islands of Arrecife Alacránes, but we found nests on Isla Chica, Isla Desertora and Isla Desterrada in July. Dinsmore and Schreiber (1974) and Schreiber et al. (1979) reported that courtship behavior in Florida begins in March and the peak of the nesting season is reached in May and June. Most young fledge in July. Our observations of pre-flight young on the islands in July indicate that the breeding cycle of Laughing Gull in the southern Gulf of México is similar to that in Florida but may begin one to two weeks earlier in the year.

We did not find direct evidence that Laughing Gull nest on other islands of the Campeche Bank reefs. However, the presence of adults and young on the islands of Arrecife Alacránes may indicate that the breeding population of Laughing Gull is increasing in the southern Gulf of México. It is too early to speculate about the effects that such an increase might have on the reproductive success of other species. However, Ansingh et al. (1960) reported that 10% of the eggs and chicks in a Sandwich Tern colony on Curaçao were lost to Laughing Gull predation. Further expansion of the Laughing Gull population on the Campeche Bank should be closely monitored.

Royal Tern (*Sterna maxima*)

Although Royal Tern breed primarily along the Atlantic and Gulf coasts, they also breed throughout the Caribbean, along the Pacific coast of México, and on the Atlantic coast of South America (A.O.U. 1998). A small breeding population also occurs in the Old World (Clapp et al. 1983). Royal Tern nest colonially on isolated and sparsely vegetated islands (Buckley and Buckley 1972).

Lowery and Newman (1954) indicated that Royal Tern did not nest on the Campeche Bank islands and Paynter (1955) found no nests during his survey in August and September 1952. However, Paynter mentioned that the lighthouse keepers informed him that Royal Tern bred on islands of Arrecife Alacránes and Cayos Arcas. Bonet and Rzedowski (1962) also mentioned that Royal Tern nested on Isla Chica and Isla Desterrada but provided no description of the colonies or the number of pairs. Fosberg (1962) found 11 nests on Isla Desterrada after causing an enormous flock, estimated to be about 1,000 birds, to take flight. Consequently, our account of the Royal Tern on Isla Chica is the second documentation that the species nests on the Campeche Bank.

When we visited the island in early July, the Royal Tern chicks were about two weeks old and were part of a crèche that contained Sandwich Tern chicks. The best time to survey the islands to determine the extent of Royal Tern nesting would be from late April through late May when the terns are most likely to be on eggs.

Sandwich Tern (*Sterna sandvicensis*)

Sandwich Tern are a cosmopolitan species, but the main concentration of breeding colonies is along the Atlantic and Gulf coasts of North America, the Atlantic coast of South America and in western Eurasia (A.O.U. 1998, Clapp et al. 1983). Throughout its range, its colonies are located on barren or sparsely vegetated sandy or shelly spits or beaches (Shealer 1999). In the southeastern United States, Sandwich Tern commonly nest in association with other terns or gulls (Shealer 1999), commonly with Royal Tern (Buckley and Buckley 1980).

Although northern Caribbean colonies are known from the United States Virgin Islands (Dewey and Nellis 1980) and Cuba (Bond 1971), little is known about the occurrence of breeding colonies in the southern Gulf of México (Clapp et al. 1983, van Halewyn and Norton 1984). Kennedy (1917) found a group of 50 Sandwich Tern nests in the midst of a large Sooty Tern colony in mid-May on Isla Pájaros. Paynter (1955) did not see any nests

during his August and September visits to Campeche Bank, but he observed many roosting on the beaches of several islands. According to Alacrán inhabitants, the main nesting colony was located on Isla Desterrada (Paynter 1955). Our observation of the Sandwich Tern nests on Isla Chica provides the first documentation in nearly 70 years that the species still breeds on Campeche Bank. We did not locate Sandwich Tern nests on Isla Desterrada and we found no historical or physical evidence to support the A.O.U. (1998) claim that Sandwich Tern nest on Cayos Arcas.

Sooty Tern (*Sterna fuscata*)

The Sooty Tern is a widely distributed species with breeding colonies on islands in tropical and subtropical waters associated with both the Atlantic and Pacific oceans (A.O.U. 1998, Clapp et al. 1983). The most comprehensive summary of known Sooty Tern breeding colonies and nesting seasons was provided by Ashmole (1963) who also detailed the nesting biology of the species. According to van Halewyn and Norton (1984), Sooty Tern are the most numerous breeding seabirds in the Caribbean region with a breeding population that exceeds 100,000 pairs. A large colony exists on the Dry Tortugas (Howell 1932, Sprunt 1954, Dinsmore 1972) where the breeding ecology was described by Watson (1966).

Several small nesting aggregations have been reported from the Gulf of México in Florida (Stevenson 1972), Mississippi (Paynter 1955), Louisiana (Purrington 1970, Portnoy 1977), and Texas (Chaney et al. 1978) and all of the islands of Arrecife Alacránes. We could not verify, however, that Sooty Tern have ever been recorded nesting on islands of Cayos Arcas as stated by Friedmann et al. (1950) and A.O.U. (1998). During our visit in April, we observed many adult Sooty Tern roosting on, and flying near, Cayo del Este but we did not find any sign of nesting activity.

Dampier (1699) was the first to record the presence of nesting Sooty Tern on Arrecife Alacránes with a description "Egg birds." Kennedy (1917) followed over two centuries later with his account of the ground "carpeted" with hundreds of nests on Isla Pájaros. Since there are so many accounts, we will summarize them by island.

Isla Perez – Although Paynter (1955) did not observe nesting during his visit, he was assured by the inhabitants of Alacrán that Sooty Tern nested by the thousands on the reef complex and Isla Perez had the largest concentration of nests. Folk (1967) was on the island in June and July 1960, and reported "myriads" of Sooty Tern nests. When Fosberg visited in July two years later, however, Sooty Tern were not nesting. Lockwood (1989) found over 20,000 Sooty Tern engaged in excavating nest scrapes on Isla Perez in April 1988. Only 1,000 nests contained eggs. Boswall found only two young left on the island in September, 1975, and Howell reported a single immature tern during his October 1984 visit. Lighthouse keepers described accounts of egg harvesting, a practice that probably continues today (Paynter 1955, Boswall 1978). Lockwood (1989) reported that 15,000 eggs were taken from Isla Perez during one year, but Boswall (1978) indicated that egg harvesting ceased after Easter each year.

Isla Chica – Bonet and Rzedowski (1962) found Sooty Tern nesting with Sandwich Tern on Isla Chica. However, they provided no details other than a brief account of the sparse vegetation at the colony site.

Isla Pájaros – The only account of nesting Sooty Tern on Isla Pájaros is that of Kennedy (1917). When he visited in May, he found eggs in late stages of incubation, but no hatchlings.

Isla Desertora – We provide the first record of Sooty Tern nesting on Isla Desertora. Although we only found 10 juvenile birds, the area appeared to have been used by a large colony.

Isla Desterrada – Both Bonet and Rzedowski (1962) and Wells (1988) report Sooty Tern colonies on Isla Desterrada.

According to Fosberg (1962), the inhabitants of Isla Perez said Sooty Tern leave in September and return each February. This is consistent with the nesting schedule described for the Dry Tortugas colony (Sprunt 1954, Watson 1966). Most nesting probably occurs from April to June and the adults and young birds may remain in the area for several months after fledging. For the remainder of the year, Sooty Tern are highly pelagic (Dinsmore 1972).

Brown Noddy *(Anous stolidus)*

Like many seabirds, Brown Noddy occur pantropically (A.O.U. 1998). Unlike many seabirds, these birds use many different habitats for colony locations (Chardine and Morris 1996) and, consequently, they occupy a large number of colony sites around the world (Clapp et al. 1983). Colonies may contain up to 50,000 pairs of birds (Clapp et al. 1983), but the majority of birds in a colony never venture far from the colony location (Watson 1908, King 1970). Some Brown Noddy populations abandon the colony site at the completion of the nesting cycle, but most remain in the vicinity of the colony throughout the year (King 1970).

A large proportion of the Atlantic Brown Noddy population nests in the Caribbean region (van Halewyn and Norton 1984). The species is widespread in the Caribbean and is the second most abundant seabird. The largest colony in the Gulf of México is located in the Dry Tortugas (Sprunt 1948, Robertson 1964, Voous 1966, Clapp and Buckley 1984, Morris and Chardine 1992). Robertson (1978) estimated that the colony contained approximately 1,500 nests but indicated that the maximum number of birds present could approach 10,000. At one time the colony may have had 35,000 birds but the number declined to about 300 by 1950 (Robertson 1964).

The colonies on Arrecife Alacránes now may exceed the Dry Tortugas colony in total numbers of breeding pairs. Paynter (1955) was the first to note that Brown Noddy nested on the Campeche Bank when he reported that over 1,000 birds were nesting on Isla Perez in September 1952. Bonet and Rzedowski (1962) and Fosberg (1962) both reported many

Brown Noddy during their visits to Isla Perez in the early 1960s. Boswall (1978) reported 2,000 adults and young associated with nests when he visited in September, but the lighthouse keeper on Isla Perez told him that these were only a fraction of the population that nested there earlier in the year. Lockwood (1989) found 2,000 Brown Noddy nests in the shrubs and low dense vegetation during his visit in April 1988.

The period of egg-laying in the Caribbean is assumed to occur from April to June (van Halewyn and Norton 1984, Morris and Chardine 1992), but we suggest that it may occur later on Isla Perez in some years. Of 1,412 nests that we examined in early July, one-third still contained eggs or chicks and several authors mentioned that eggs were still present in the colony as late as September.

DISCUSSION AND CONCLUSIONS

Ornithologically, the Gulf of México is a tropical sea (Lowery and Newman 1954). The majority of its breeding pelagic avifauna consists of species that approach the northern limits of their normal breeding range. The southern Gulf of México remains one of the areas of the world least understood ornithologically. Although colonies of breeding seabirds have long been known from the islands on the Campeche Bank reefs, most investigators have reported relatively small breeding populations. The Campeche Bank islands are significant nesting areas for marine birds, and the seabird populations in the Gulf of México are much larger than previously believed.

There are many problems associated with the estimation of tropical seabird populations (Schreiber and Schreiber 1986). Our estimates of colony size were made conservatively, but our numbers may be further limited because all of our observations of nesting birds were diurnal. Several researchers (Kepler 1969, Schreiber and Schreiber 1986, Clapp 1990) noted that populations of birds roosting at night on Pacific islands were much larger than those seen during the day. For example, Schreiber and Schreiber (1986) demonstrated that estimates of tern nests on one Pacific atoll might underestimate total numbers of terns by two orders of magnitude and the maximum number of birds seen at any one time could represent only about 5% of the total number of terns using the atoll throughout the year. If a similar relationship between bird counts and total annual use exists on the islands in the southern Gulf of México, the estimate of 13,570 adult Sooty Tern seen during the day on Isla Perez in July 1986 might signify a much higher number using the island annually.

The islands of the Campeche Bank may serve as habitat bases for interactive metapopulations of seabirds. The term "metapopulation" was originally coined by Levins (1969, 1970) to describe the interactions of insect subpopulations in patchy environments. Since the original description of the term, the concept of metapopulations has been expanded to include any situation in which subdivided populations are distributed as discrete, interbreeding units that regularly occupy, then abandon, habitat patches (Gilpin and Hanski 1991, McCullough 1996). Insular-nesting seabirds in restricted geographic regions meet all of the criteria for metapopulations (Buckley and Downer 1992).

Although the historical record of the seabird colonies on the Campeche Bank is fragmented and sparse, patterns of colony use and abandonment are evident. Frequent alternations of site use and abandonment may be common in organisms that are obligatorily colonial (Buckley and Buckley 1972, Buckley and Downer 1992). Seabirds may change nesting locations in concert with shifting food resources or in response to local disturbances. Unless the species practices group adherence (Buckley and Buckley 1980), the individuals or pairs that constitute a colony also will change each time a colony is abandoned and relocated.

If the seabirds of the Campeche Bank do comprise metapopulations, the dynamics of the situation likely produce beneficial effects. Disturbances that have occurred on some islands have been offset by population shifts to other locations within the Campeche Bank complex. As a result, populations of seabirds in the southern Gulf have remained relatively stable. It is unfortunate that such large populations of seabirds have been so overlooked by the scientific and conservation communities. The islands of the Campeche Bank should be surveyed on a regular basis and human use of the islands should be curtailed to the maximum extent possible.

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ATOLL RESEARCH BULLETIN

NO. 483

A CENSUS OF SEABIRDS OF FRÉGATE ISLAND, SEYCHELLES

BY

ALAN E. BURGER AND ANDREA D. LAWRENCE

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
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JUNE 2000

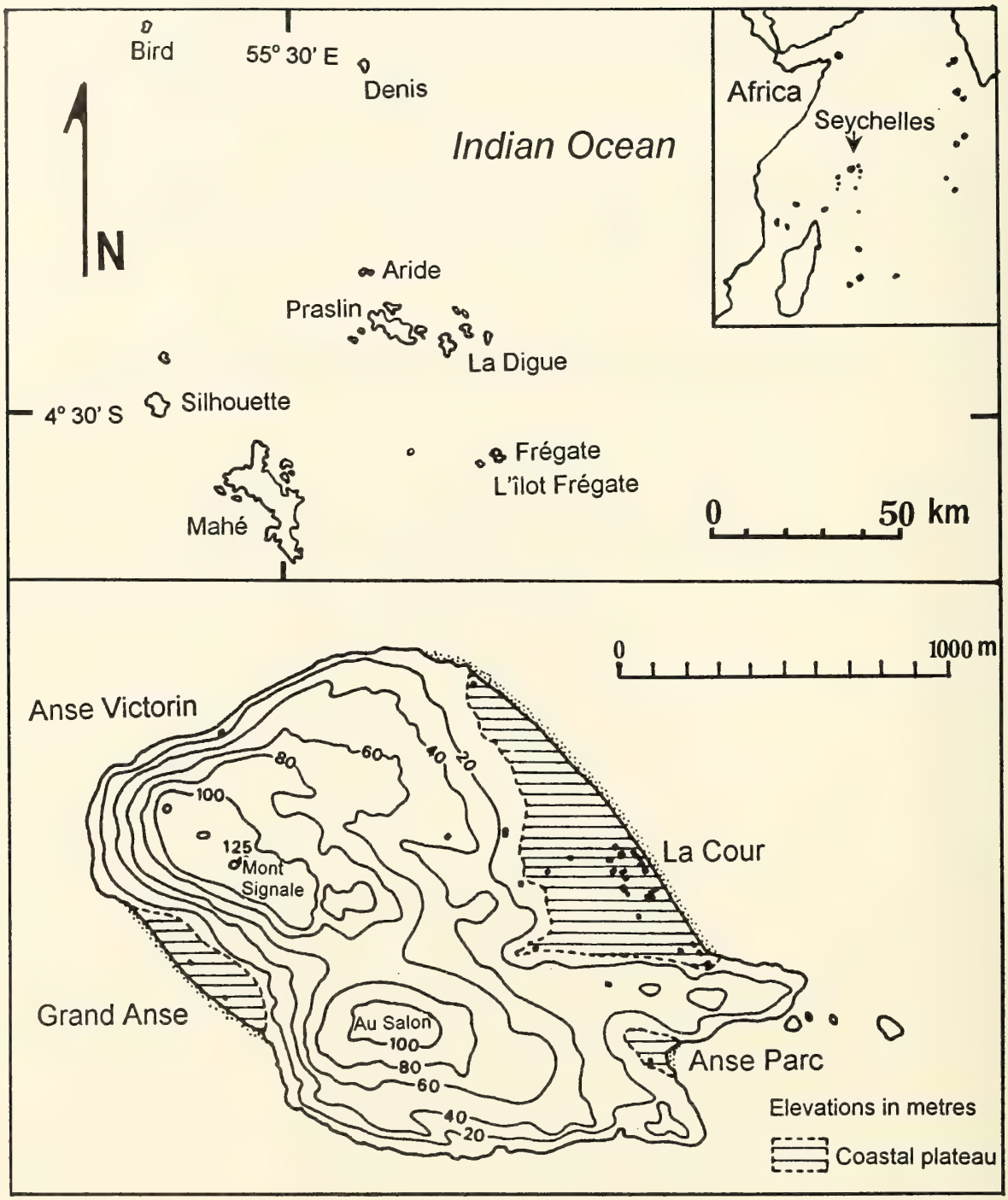

FIGURE 1. Index map showing the location of Frégate Island, Republic of Seychelles. The lower map shows the topography of Frégate Island, based on Robertson and Todd (1983).

A CENSUS OF SEABIRDS ON FRÉGATE ISLAND, SEYCHELLES

BY

ALAN E. BURGER[1,2] and ANDREA D. LAWRENCE[1]

ABSTRACT

We censused seabirds on Frégate Island, Seychelles, from 4 to 8 August 1999, to monitor changes expected from forest restoration and rat eradication. Lesser Noddies (*Anous tenuirostris*) nested in mixed woodland, scattered alien and native trees among plantations and in four clumps of banyan trees (*Ficus benghalensis*). Our count of 7,300 Lesser Noddy nests (95% confidence limit ± 1,550) was almost three times higher than a previous estimate of 2,700 pairs. The actual total in 1999 was probably more than 8,000 nests because some nests had already fallen from trees by the time we did our census. White (Fairy) Terns (*Gygis alba*) were more widespread, nesting principally in mixed exotic woodland, scattered trees among buildings and plantations, sang-dragon (*Pterocarpus indicus*) woodland, and in banyan trees. Our estimate for White Terns was 3,030 nests (95% CL: ± 980 nests), and the year-round breeding population was several times higher. Frégate thus supports one of the largest populations of White Terns in the Seychelles. We found only two nests of White-tailed Tropicbirds (*Phaethon lepturus*) and estimated the total breeding population at less than 20 pairs. A search was made by day and at night for shearwaters, but there was no evidence of their breeding. No other seabirds appear to be breeding on Frégate. We recommend regular monitoring of the noddy and tern populations. Shearwaters and other ground-nesting seabirds are likely to re-colonize Frégate if rats are eradicated.

INTRODUCTION

Frégate Island is generally not considered among the most important seabird colonies in the granitic Seychelles, although there were once large numbers of seabirds breeding there (Rocamora and Skerrett, In Press). Breeding seabirds have been severely affected by over a century of human habitation, removal of indigenous forest, the presence of feral cats and, more recently, rats. The current owner of the island is attempting to restore some of the indigenous forest and a rat eradication program was initiated in 2000. With these changes Frégate might once again become one of the larger

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seabird colonies in the Seychelles. Our study provides baseline data to monitor these changes and to help understand the restoration of tropical seabird colonies.

Three seabird species were known to breed in 1997: an estimated 2,700 pairs of Lesser Noddy (*Anous tenuirostris*), "thousands of pairs" of White (Fairy) Terns (*Gygis alba*), and an unknown number of White-tailed Tropicbirds (*Phaethon lepturus*) (Rocamora and Skerrett, In Press). The small satellite island, L'îlot Frégate, which we did not visit in 1999, supports breeding populations of Sooty Tern (*Sterna fuscata*), Bridled Tern (*S. anaethetus*) and Brown Noddy (*Anous stolidus*). We counted seabirds on Frégate Island over five days, 4-8 August 1999. Although incomplete, our census provides the most detailed account of present seabird populations for this island. We show that Frégate is an important colony for White Terns and appears to have a growing population of Lesser Noddies.

STUDY AREA AND HABITAT DIVISIONS

Frégate Island (4°35' S, 55°56' E) is 202 ha in area, most of which is gently sloping hillside with two hills reaching 125 and 100 m elevation (Fig. 1). The island's topography, history and vegetation are described by Robertson and Todd (1983), McCulloch (1994, 1996) and Rocamora and Skerrett (In Press). Virtually all of the indigenous forest was removed over the past 100 years and replaced by alien trees, including coconut (*Cocos nucifera*), cinnamon (*Cinnamomum zeylandicum*), cashew (*Anacardium occidentale*), breadfruit (*Artocarpus altilis*), sang-dragon (*Pterocarpus indicus*) planted to support vanilla vines, citrus and other fruit trees. Several huge multi-stemmed banyan (*Ficus benghalensis*) trees grow in the hillside forest and as isolated clumps on the northeast plateau and southwest coast. Thickets of coco-plum (*Chrysobalanus icaco*) shrubs cover most of the open woodland and unforested hillside.

The present owner is reestablishing native trees in parts of the forest, but nearly all the forest remains dominated by alien crop trees. Most of the lowland coastal plateau is used for agriculture, buildings, roads and service areas, but many large trees in this area support nesting terns and noddies. Feral cats (*Felis catus*) almost certainly affected seabirds on Frégate, especially ground-nesting species, before they were eradicated in 1982 (Watson et al. 1992). Norway rats (*Rattus norvegicus*), which were accidentally introduced to Frégate in 1994, likely had similar impacts. Rats were widespread and abundant in 1999, but a program to eradicate them was underway in mid-2000.

We used the coarse-scale habitat map made by McCulloch (1996) modified by our own measurements and field observations (Fig. 2). We could not accurately map or estimate the areas of the various habitat patches due to the absence of aerial photographs. When better estimates of habitat patch size are possible from a high-quality aerial photograph, our estimates of nest density can be reapplied to give more accurate measures of seabird populations. Our preliminary inspection, along with the experience of James Millett, the resident biologist on Frégate, suggested that very few or no seabirds nested in the large areas of scrub/grassland or the riverine bamboo. White Terns nested in very low densities in the disused coconut plantation but we did not have time to sample

FIGURE 2. The upper map shows the distribution of the major habitat types on Frégate Island (modified after McCulloch 1996). The lower map shows the blocks of habitat sampled for seabirds in August 1999, including mixed exotic woodland (areas A-C), sang-dragon woodland (areas D-F), plantation, hotel and service areas on the plateau (areas G, H, I and J); and isolated clumps of banyan trees (areas K, L, M and N). Transect lines used for locating sample plots in woodland habitats are also shown.

this widespread habitat. Likewise, we were unable to check all the scattered albizia (*Albizia falcata*) trees, in which a few White-tailed Tropicbirds nested.

We used stratified sampling, focusing on four habitat types: mixed exotic woodland (Fig. 2, areas A, B, C); sang-dragon woodland (areas D, E and F); plantation, hotel and service areas on the plateau (areas G, H, I and J); and isolated clumps of banyan trees (areas K, L, M and N). McCulloch (1996) classified the woodland near the airstrip (Fig. 2: area A) as sang-dragon woodland, but our sample plots here included a diversity of tree species and so we classified this as mixed exotic woodland. The density of White Terns was higher here than on the hill slopes and so was treated separately.

SAMPLING METHODS

Census units – For Lesser Noddy we counted all nests, whether occupied or not. At the time of our census some noddies had already lost eggs or chicks and it was impossible to determine the original number of active nests. Most noddy nests were high in trees making it impossible to see their contents. For White Terns we counted chicks and incubating adults (evidence of the egg was usually obvious from the hunched, immobile posture of the adult and the pouching of the breast feathers over the egg) to get the number of active pairs.

Census Methods Used for Terns and Noddies.

Plot sampling – This method was used in the mixed exotic woodland and sang-dragon woodland. We estimated the density of nests within representative sample plots and then applied the mean density to larger areas of habitat to estimate the total number of nests. All nests were counted within 300 m^2 circular plots (radius 9.77 m) with the plot centers randomly spaced along transect lines. The first plot was placed 10-30 m from the habitat edge to ensure that it was entirely within the sampled habitat. To avoid overlap, the subsequent plots were placed 20-40 m apart. The actual distances between plots were determined by computer-generated random numbers within these intervals. Transect lines followed fixed compass bearings (NE to SW, or NW to SE) and were 50 m apart in exotic woodland area A and in sang-dragon woodland areas E and F, but 100 m apart in the larger exotic woodland area C (Fig. 2). To sample the narrow strip of mixed woodland in area B, we followed the path from the ridge crest to the lower road, with plots placed 20-40 m apart along the path and 10-30 m perpendicular to the path on alternating sides (left or right) of the path.

Direct counts – Plot sampling was not suitable for counting nests in the scattered trees in the plantation/hotel area (Fig. 2, areas G-J) nor in the banyan clumps (areas K-N). Here we counted the nests in each individual tree.

RESULTS

Lesser Noddy – Lesser Noddy nests were found in three areas: within the mixed exotic woodland bordering the airstrip (Fig. 2, area A); on scattered trees on the NE plateau among the buildings and service areas (areas G-J), particularly around the marina; and in four clumps of very large banyan trees and nearby *Pisonia grandis* trees (areas K-N). No

noddy nests were seen in the mixed exotic woodland, sang-dragon woodland or the disused coconut plantation on the hillside.

A total of 7,302 nests of Lesser Noddies were found (Table 1). Most nests were from direct counts involving no confidence limits, but the small area of woodland sampled had 95% confidence limits of ± 1,545 nests (858.3 nests per ha x 1.8 ha). The estimated population (rounded to the nearest 10) was thus 7,300 ± 1,550 nests.

White Tern – White Terns were more widespread than the Lesser Noddies (Table 1), occurring in the mixed exotic woodland (1,601 nests), sang-dragon woodland (793 nests), plantation/hotel area (564 nests) and banyan clumps (68 nests). Overall, a total of 3,026 nests were counted. The combined 95% confidence limit for the three habitats in which plot samples were used (plateau mixed woodland, hillside mixed woodland and sang-dragon woodland) was calculated from the standard deviations in each habitat, using the habitat areas for weighting and the method outlined in Sutherland (1996:101-105). The resulting 95% confidence limit was ± 977 nests. There were no confidence limits for the direct counts in the plantation/hotel area and banyan clumps. The rounded estimate of White Tern nests in the areas surveyed was thus 3,030 ± 980 nests. Since White Terns breed all year round, the current breeding population represents only a portion, likely less than half, of the total year-round breeding population. This total is thus likely to exceed 6,000 pairs.

White-tailed Tropicbird - We saw two tropicbird nests. One was 3 m high in a cavity on top of a large stump at the edge of vegetable gardens on the northeast plateau. The second was in a cavity 4 m high in a large red sandalwood (*Adenanthera pavonina*) tree, on the ridge in area B (Fig. 2). Both nests were found only because the adults' tails were visible. Other nests, especially those with chicks, would not be as readily visible and there were probably some in the large banyan trees. Judging by the number of nests found, the availability of suitable nest sites and the numbers of adults flying over the island, we estimate that the total breeding population is less than 20 pairs. After our visit one pair attempted nesting on the ground among the hotel buildings but failed (J. Millett, pers. comm.). Widespread ground nesting, as used by the majority of tropicbirds in the Seychelles, is unlikely until rats are removed from Frégate.

Shearwaters and other seabirds – We made intensive searches of the grassy slopes and rocky areas of both peninsulas on the southeast end of the island and on the hilltop at Mont Signale (Fig. 1). These are habitats in which Wedge-tailed Shearwaters (*Puffinus pacificus*) and Audubon's Shearwaters (*P. lherminieri*) might nest. We also searched the peninsulas at night using head lamps and listened for calls. We found no signs of nesting shearwaters. There were signs of burrowing beneath some large boulders and in a few grassy spots but these were obviously made by rats and not shearwaters (evidence of rat droppings, no distinctive shearwater smell, and no response to imitated shearwater calls). A few Wedge-tailed Shearwaters were seen by day flying past the island. In November and December 1999, during the northwest monsoon breeding season, J. Millett heard Wedge-tailed Shearwaters calling over the forest at night and found several on the ground, but no nests.

Table 1. Estimated number of Lesser Noddy and White Tern nests in census areas on Frégate Island in August 1999. See Fig. 2 for habitat areas.

				Lesser Noddy		White Tern	
Habitat	Map area	Location	Habitat area (ha)	Nest density (Nests/ha)	Total nests	Nest density (Nests/ha)	Total nests
Mixed exotic woodland							
	A	Plateau at airport	1.8	770.8	1387	175.0	315
	B	Slope near staff housing	2.5	0	0	55.9	140
	C	Slope above garden fields	20.5	0	0	55.9	1146
Total mixed exotic woodland			24.8	-	1387	286.8	1601
Sang-dragon woodland							
	D	Slope above new hotel	1.6	0	0	111.7	179
	E	Slope near Au Salon	4.3	0	0	111.7	480
	F	Slope near Anse Parc	1.2	0	0	111.7	134
Total sang-dragon woodland			7.1	-	0	335.1	793
Hotel/Plantation							
	G	NW of Plantation house	-	-	443	-	111
	H	Plantation house to marina	-	-	415	-	196
	I	Marina area	-	-	2530	-	177
	J	Trees around fields	-	-	428	-	80
Total hotel/plantation			-	-	3816	-	564
Banyan clumps							
	K	Pirate's Wall	-	-	579	-	3
	L	Near Pirate's Wall	-	-	116	-	4
	M	Anse Coup de Poing	-	-	1069	-	33
	N	Anse Parc	-	-	335	-	28
Total banyan clumps			-	-	2099	-	68
TOTAL ALL AREAS					**7302**		**3026**
± 95% confidence limits (see text)					1545		977

There was no evidence that any other seabirds nested on the island. Brown Noddies and Sooty Terns were seen on a few occasions passing near the island but these were likely from L'îlot Frégate or some other colony.

DISCUSSION

Our five-day visit was insufficient to make a detailed inventory of the seabirds on Frégate, but our survey included all of the Lesser Noddy nesting areas and most of those of White Terns. We were unlikely to have missed any concentrations of nesting seabirds. The disused coconut plantation, which we did not sample, supported some tern nests, but based on our observations of the habitat and the number of terns seen in and over that habitat, the total there was less than 200 pairs. We almost certainly missed some White-tailed Tropicbird nests because those high in the trees would be very difficult to see but, based on the numbers of adults seen flying overhead, the total population seems likely to be around 20 pairs at most. Other seabird species appeared to be absent from Frégate.

Our results show that Frégate has a more important seabird colony than previously expected. Our count of Lesser Noddy nests (7,300 ± 1,550) is almost three times higher than a previous estimate of 2,700 pairs (Rocamora and Skerrett, In Press). This estimate seems to be based on unpublished counts of nests made by C. Murray and M. Nicoll in late August to early September 1997 (Frégate Island unpublished data). Their count was made several weeks later than ours and this partly explains the lower count in 1997. Lesser Noddies nest synchronously in Seychelles and there is very little replacement of lost eggs or fallen nests. It is not possible to determine from Murray and Nicoll's notes whether they covered the same areas as we did. Our census was made when many noddy nests had already fallen off the trees so the maximum count in 1999 was likely more than 8,000 nests. This was considerably less than the large Lesser Noddy colonies elsewhere in the Seychelles, on Aride Island (108,000-166,000 pairs in 1996-1998; Betts 1998, Bowler and Hunter 1999), Cousin Island (82,000 pairs in 1999; Burger and Lawrence, unpublished) and Cousine Island (60,000 pairs in 1999; G. Wright, pers. comm.). Nevertheless, our data show that the Frégate colony is worth monitoring. There is no shortage of nesting habitat on Frégate and the colony could easily increase manyfold.

Frégate is even more important as a colony for White Terns. A comparison of the number of nests per census on Frégate and other colonies on the granitic Seychelles is given in Table 2. Comparisons of White Tern populations are difficult because the species nests year-round in Seychelles, and hence the total breeding population is much larger than a count made at any one time. The proportion breeding at any single point in time is unknown. Comparing these "snapshot" counts is a more precise way to compare islands than using extrapolations of such counts to year-round populations. This comparison shows that Frégate has a population of White Terns similar to that of Aride, and larger than the populations on Cousin and Cousine Islands. Clearly, Frégate must be included in any consideration of the White Terns in Seychelles. Our census should be repeated at other times of the year to get a better idea of the year-round breeding density.

Our impression, having observed White Terns on several of the Seychelles islands, is that chicks on Frégate were more frequently fed large prey items (usually a single flying fish or other species) than on these other islands. Frégate is the easternmost of the granitic islands and the White Terns there might be exploiting different prey stocks than those from the more central islands. We were also surprised at the high density of White Tern nests in localized areas on Frégate, particularly in breadfruit and other trees among the buildings and the plantation on the northeast plateau. Several dozen nests

were often visible from one point. Clearly this would make an excellent study site for this species.

Table 2. Comparison of populations of White Terns on four granitic islands in the Seychelles. Each count is the breeding population at the time of the census and not the year-round total of breeders.

Island	Year	Month	No. of nests	95% confidence limits	Source
Frégate	1999	Aug	3030	980	This study
Aride	1996	Jan/Feb	6795	1424	Betts 1998
Aride	1996	Jun	1945	536	Betts 1998
Aride	1997	Jan	5040	1371	Betts 1998
Aride	1997	Jun	1686	561	Betts 1998
Aride	1998	Jan/Feb	3204	797	Bowler and Hunter 1999
Aride	1998	Jun	1664	539	Bowler and Hunter 1999
Mean for Aride			3389		
Cousin	1989	Mar/Apr	2512	-	Braat et al (1989)*
Cousin	1990	Feb	1751	-	Den Boer and Geelhoed (1990)*
Cousin	1999	May	1079	242	Burger and Lawrence (unpubl.)
Cousin	1999	Jun/Jul	1405	251	Burger and Lawrence (unpubl.)
Cousin	2000	Feb	3606	709	Burger and Lawrence (unpubl.)
Mean for Cousin			2071		
Cousine	1999	Jul	1278	282	G. Wright and K. Passmore (unpubl.)

*The means for Cousin in 1989 and 1990 were recalculated from the raw data in these two reports, and not using the erroneous methods used by the authors.

There are few previous data on the seabirds of Frégate. Stoddart (1984) and Diamond (1994), respectively, refer to 24,000 and 15,000 pairs of Brown Noddy nesting on Frégate in 1955, but these figures almost certainly refer to the population on nearby L'îlot Frégate, where Rocamora and Skerrett (In Press) give the combined total of Brown Noddies and Sooty Terns as more than 25,000 pairs.

CONCLUSIONS AND FUTURE WORK

Our brief visit showed that Frégate supports significant breeding populations of Lesser Noddies and, especially, White Terns. Frégate should no longer be ignored as a

seabird colony in the granitic Seychelles. If the habitat management at Frégate proceeds as planned, with eradication of rats and reforestation with indigenous trees, then Frégate will become more suitable for these and other seabirds. Ground- or burrow-nesting species, such as Brown Noddy, Bridled Tern, Sooty Tern, Wedge-tailed Shearwater and Audubon's Shearwater are likely to colonize the island and tropicbirds will increase. We recommend regular monitoring of the existing seabird populations plus continued searching for evidence of other seabirds. L'îlot Frégate should be included in future censusing and monitoring. Monitoring the changes in seabird populations caused by habitat restoration or the removal of alien predators is important in evaluating the benefits of these procedures and in understanding the losses caused by earlier human interference.

ACKNOWLEDGEMENTS

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ATOLL RESEARCH BULLETIN

NO. 484

CORAL AND FISH COMMUNITIES IN A DISTURBED ENVIRONMENT: PAPEETE HARBOR, TAHITI

BY

MEHDI ADJEROUD, SERGE PLANES AND BRUNO DELESALLE

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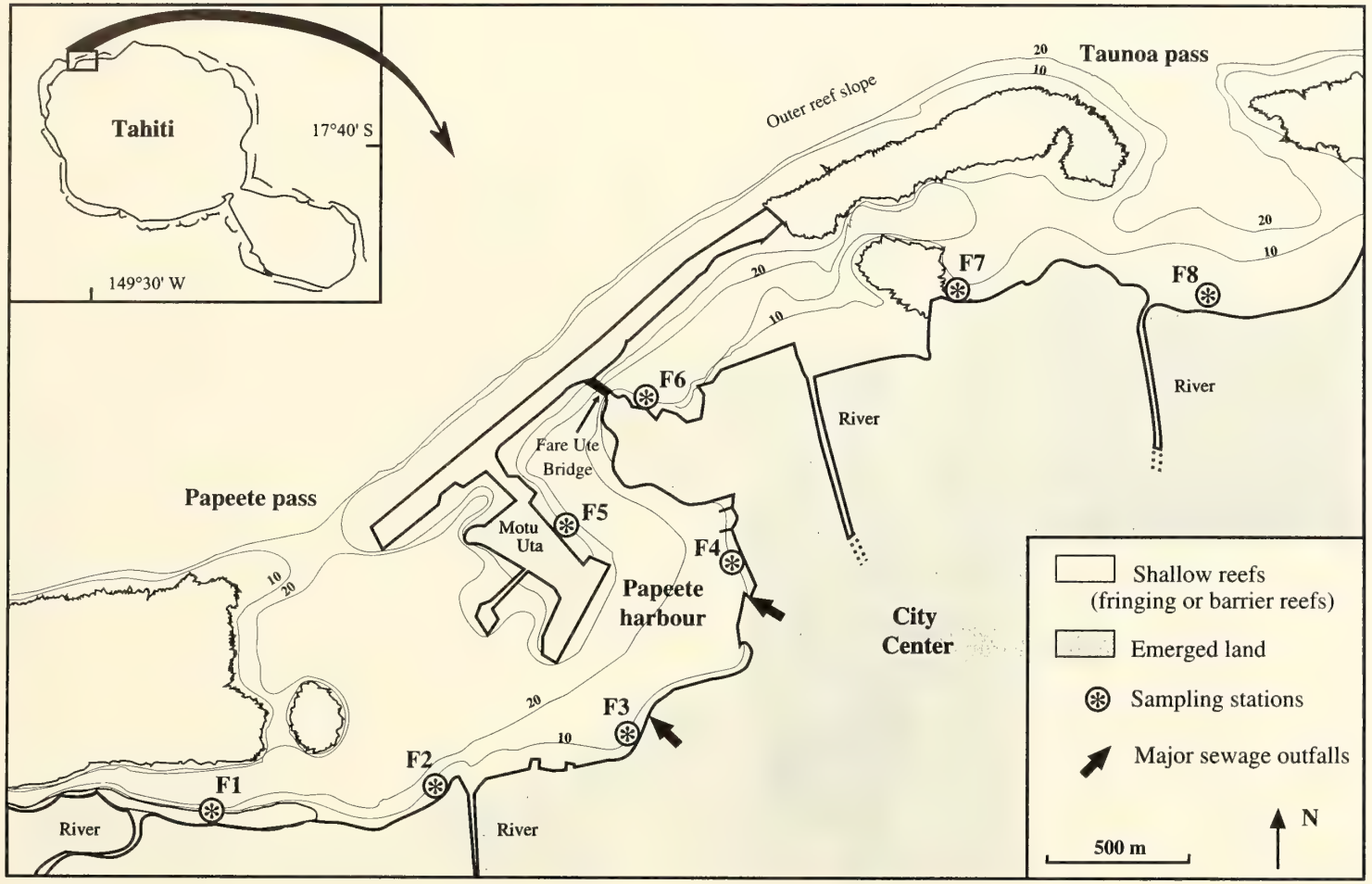

Figure 1. Map of the Papeete harbor vicinity; the eight sampling stations (F1 to F8) are indicated by asterisks.

CORAL AND FISH COMMUNITIES IN A DISTURBED ENVIRONMENT: PAPEETE HARBOR, TAHITI

BY

MEHDI ADJEROUD[1], SERGE PLANES[1], and BRUNO DELESALLE[1]

ABSTRACT

A total of 104 fish and 24 coral (Scleractinia, Zoanthidea, Corallimorpharia, Milleporina) species were identified in the area of Papeete harbor (Tahiti, French Polynesia). This overall richness is comparable to less-disturbed fringing reefs around high volcanic islands in the Society Archipelago. Human activities reduced species richness slightly in inner areas of the harbor. Two passes, which connect the harbor to the open ocean, renew lagoonal waters in the inner harbor at a rate that appears sufficient to minimize effects of human disturbance.

INTRODUCTION

Reef communities are highly sensitive to a wide range of human-induced disturbances (Nishihira, 1987; van Woesik, 1994; and Green et al., 1997). Mining and dredging operations constitute one of the most obvious potential threats to reef communities (Dodge and Vaisnys, 1977; White, 1987; Brown et al., 1990; and Rogers, 1990). The impact of sediment disposal from dredging on reef communities varies according to factors such as the degree of resulting turbidity and the presence of toxic substances in dredged materials (Rogers, 1990). Nutrient enrichment by sewage effluent generally enhances benthic and planktonic algal biomass and primary production, which reduces coral abundance and favors benthic filter-feeding invertebrates (Pastorok and Bilyard, 1985; and Tomascik and Sander, 1987). Toxic effects, such as metabolic changes, decreased growth and reproduction (Pastorok and Bilyard, 1985), may result from chemicals commonly found in sewage effluent (metals, PCBs, chlorine, pesticides, and petroleum hydrocarbons). Although large discharges of effluent into poorly flushed lagoons and bays have caused major changes in reef community structure (Pastorok and Bilyard, 1985), little or no impact has been observed on some well-flushed reefs that received small quantities of effluent. While human-induced disturbances result in generally declining reefs in harbors, the construction of a harbor in Diego Garcia Atoll had no major or lasting effect on coral diversity or coral cover (Sheppard, 1980).

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In French Polynesia, spatial and temporal patterns of macrobenthic invertebrates and fish assemblages are well documented on fringing reefs, barrier reefs, and outer-reef slopes surrounding high volcanic islands (Galzin, 1987; Adjeroud, 1997; and Augustin et al., 1997). In contrast, reefs in harbor locations have been largely ignored. The aim of the present study was to examine the status of coral and fish communities in Papeete harbor.

METHODS

With approximately 93,000 inhabitants, the city of Papeete and its suburbs are by far the most populated area in French Polynesia. Papeete harbor was built on both sides of a deep channel connecting Papeete pass and Taunoa pass (Fig. 1). The ocean side of the harbor was built by extension of a small islet (Motu Uta), and is connected to the island side by Fare Ute Bridge. The island side of the harbor is adjacent to the city center. In operation since the end of the 19th century, the harbor was subjected to extensive construction and development during the 1960's. This development persisted into the 1980's with total freight traffic increasing from 600,000 tons in 1977 to 1 million tons in 1987.

Eight stations were established in the study area (Fig. 1). Stations F3, F4, F5, and F6 were located in the inner part of the harbor, whereas stations F1, F2, F7 and F8 were located at its margin. A station was defined as an area of approximately 250 m^2 (10 25), starting from the shore down to a depth of 5 m. At each station, one qualitative survey (presence/absence) of fishes was made by Planes by snorkeling or diving during a 60-minute period of observation on the area covered by the station. The same method (i.e., 60-minute period of observation) was used by Adjeroud for the qualitative survey of anthozoans (including hard and soft corals and *Millepora*, herein classified as corals). Qualitative surveys were made in August 1995 (dry season). Surveys of surface-water quality characteristics at the same eight stations were made once a year at the beginning of the rainy season (November) from 1990 to 1995 by the Laboratoire d'Etudes et de Surveillance de l'Environnement (LESE). Temperature, salinity, pH, and dissolved oxygen were measured using *in situ* probes. Surface-water samples were collected for measurement of suspended matter, nutrients (NH_4, NO_2, NO_3, PO_4, SiO_2), and heavy metals (Fe, Cu, Zn). Additional details on water-survey methodologies are given in Langomazino et al. (1993).

Classification analysis (CA) was used to examine the variation in species composition among stations.

RESULTS

Fish and coral communities

A total of 104 fish species representing 25 families was recorded at the eight stations (Table 1). Dominant families were Labridae (20 species), Pomacentridae (16 species), Acanthuridae (13 species), and Chaetodontidae (12 species). Species richness varied from 28 to 51 species per station. The lowest species richness was found in the inner part of the harbor (stations F4 and F6). Highest species richness was found at stations F1, F2, and F8 located at the margin of the harbor. Seven species were observed

stations F1, F2, and F8 located at the margin of the harbor. Seven species were observed at all eight stations, whereas 32 species were each observed at only one station. Classification analysis showed that F8 and F3 had a distinct species composition with several species not observed elsewhere in the harbor. Species composition at other stations was more similar, particularly at F5, F6, and F7 (Fig. 2).

A total of 24 coral species representing four orders (Scleractinia, Zoanthidea, Corallimorpharia, Milleporina) was recorded during this survey (Table 2). Species richness varied between 8 and 15 species per station. As with fishes, the highest species richness was found at the margin of the harbor (stations F1, F6, F7, and F8). Two species were observed at all eight stations and five species were each restricted to one station. Because they were mainly composed of common species, species assemblages at stations F2, F5, F7, and F8 were highly similar (Fig. 2). In contrast, stations F1 and F6, which contained several species not observed elsewhere in the harbor, had distinct species compositions.

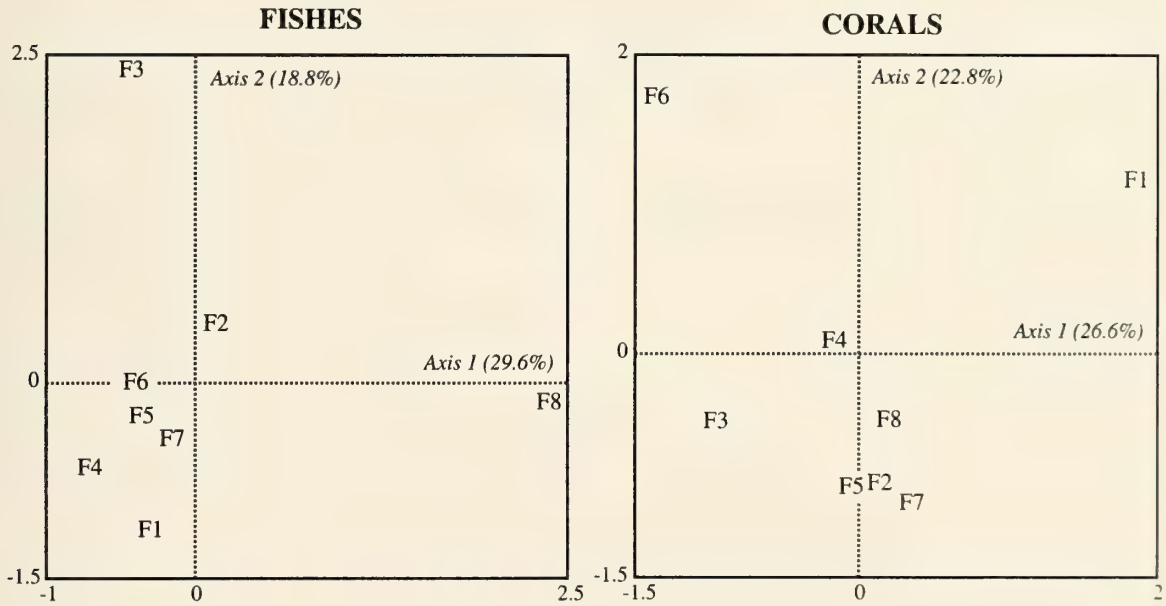

Figure 2. First two axes of the classification analysis performed on coral and fish species composition recorded at the eight stations. The inertia of each axis is given.

Water quality survey

Mean values of temperature, pH, NO_2, suspended matter, and Cu concentrations were quite similar among stations (Table 3). Dissolved oxygen concentrations were also similar among stations except for station F3 where the mean value was slightly higher.

Stations F3 and F7 were characterized by lower salinities and higher concentrations of SiO_2, indicating that these stations were subjected to higher terrestrial influences. Stations F3 and F7 were also characterized by high NO_2, NH_4 and PO_4, and Fe concentrations.

DISCUSSION

With 104 fish species and 24 coral species identified, the overall richness in the area of Papeete harbor is not dramatically different when compared with less-disturbed fringing reefs surrounding high volcanic islands in the Society Archipelago. In Moorea, 24 coral and 141 fish species were recorded on the lagoonal fringing reefs surrounding the island, and 33 coral and 112 fish species were observed on the fringing reefs bordering Opunohu Bay on the north coast of the island (Galzin, 1987; Adjeroud, 1997; and Planes, unpubl. data). Variation in species composition of coral and fish assemblages within Papeete harbor was moderate. Dissimilarities among stations were caused mainly by the addition of several occasional species (i.e., observed at one or two stations), but not by a substitution of species. Moreover, most of the species observed within the harbor are commonly found on fringing and barrier reefs around high volcanic islands in the Society Archipelago. Thus, no particular species, such as introduced species imported by transoceanic shipping (Carlton, 1987), were found in Papeete harbor, nor were any possible "indicator" species missing from inner-harbor stations.

Despite a reduction in the number of species observed in the inner part of Papeete harbor where human activities are concentrated, a minimum of 28 fish and 8 coral species was found. We may conclude that harbor and human activities in Papeete induced only a slight reduction in species richness; this reduction was restricted to the inner part of the harbor as was also observed in Castle Harbor, Bermuda (Dodge and Vaisnys, 1977). We suspect that the weak and localized impact of harbor and human activities is a function of water circulation in the area. Water enters the lagoon primarily by Papeete Pass and exits by Taunoa Pass resulting in an eastward current (De Nardi et al., 1983). A reverse tide-phase current is sometimes observed, mainly during the dry season (May to September). The mean current speed at Fare Ute Bridge was estimated at 0.35 $m.s^{-1}$ during the wet season, but can exceed 1.00 $m.s^{-1}$ under strong winds (De Nardi et al., 1983). These currents drove a flow estimated as 200-600 $m^3.s^{-1}$. From these flow estimations, it can be deduced that the entire volume of the inner part of the harbor is renewed in 4 to 12 hours. This hydrodynamic pattern seems sufficient to prevent confinement of waters to the inner part of the harbor, which may alleviate any resulting harsh hydrological conditions that might develop given the nature and extent of human activities.

The number of fish and coral species per station was not significantly correlated with any of the hydrological factors selected in this study (Pearson correlation coefficient, $p>0.05$). The rapid renewal of lagoonal waters may help explain why the hydrological factors considered here had rather weak explanatory power. In fact, the mean values of several factors (salinity for example) did not reach extreme values such as those that are associated with a reduction in number of species in bayheads of Moorea (Adjeroud, 1997). Other factors did not vary significantly among stations as was also

shown by Langomazino et al. (1993). The variation in species composition and richness in Papeete harbor that we did find is likely due to other unmeasured environmental factors, such as extent of adequate substrate and habitat for recruitment, nature and level of sedimentation, and biotic interactions. Additional measurements of abiotic factors in the water column and in the substrate therefore are needed to allow us to identify more clearly possible factors influencing the distribution of species in this area.

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Table 1. Fish species recorded at the eight stations in Papeete harbor. The location of the stations is presented in Fig. 1.

Species	Stations							
	F1	F2	F3	F4	F5	F6	F7	F8
Saurida gracilis								+
Myripristis sp.	+	+		+	+	+	+	
Neoniphon aurolineatus	+							
N. sammara	+			+	+			
Aulostomus chinensis	+	+		+		+		
Fistularia commersonii			+					
Pterois radiata							+	+
Cephalopholis argus	+							
Epinephelus merra	+	+	+	+	+	+	+	+
Cirrhitus pinnulatus								+
Paracirrhites arcatus								+
Apogon fraenatus			+					
A. kallopterus					+		+	
A. sp.							+	
Cheilodipterus quinquelineatus			+		+	+		
Caranx melampygus		+	+					
C. sexfasciatus				+		+	+	
Lutjanus fulvus	+	+	+	+	+	+		
Caesio caerulaurea	+	+	+		+		+	
Gnathodentex aureolineatus	+		+			+	+	
Monotaxis grandoculis		+	+	+	+	+		
Mulloides flavolineatus			+					
M. vanicolensis			+					
Parupeneus barberinus	+	+		+	+	+	+	
P. ciliatus	+	+		+				
P. multifasciatus	+	+	+		+	+	+	+
Chaetodon auriga				+			+	
C. citrinellus	+			+		+		
C. decussatus	+			+	+	+	+	
C. flavirostris	+	+					+	+
C. lunnutatus	+	+		+			+	
C. lunula								+
C. ornatissimus	+	+	+	+	+	+	+	+
C. reticulatus						+		
C. ulietensis	+	+	+	+	+	+	+	+
C. unimaculatus	+							
Forcipiger flavissimus	+	+	+		+		+	+
Heniochus chrysostomus		+	+			+		
Centropyge flavissimus	+	+	+	+	+	+		
Abudefduf septemfasciatus		+	+		+		+	
A. sexfasciatus	+				+		+	+
A. sordidus	+							
Chromis iomelas								+
C. margaritifer								+
C. vanderbilti	+		+		+		+	
C. viridis		+						+
Chrysiptera leucopoma	+		+	+	+	+		
Dascyllus aruanus	+				+			+
D. trimaculatus								+
Plectroglyphidodon leucozona	+		+	+	+	+	+	

Pomacentrus pavo		+	+			+	+	+
Stegastes albofasciatus		+						
S. fasciolatus								+
S. lividus	+	+	+	+	+	+	+	
S. nigricans		+						
Anampses caeruleopunctatus								+
Bodianus axillaris		+	+					
Cheilinus chlorourus	+		+					
C. trilobatus	+	+		+				
Epibulus insidiator	+							+
Gomphosus varius		+						+
Halichoeres hortulanus		+						+
H. margaritaceus		+	+			+		+
H. marginatus								+
H. ornatissimus					+	+	+	
H. trimaculatus	+	+						+
Labroides bicolor	+	+					+	+
L. dimidiatus								+
Pseudocheilinus hexataenia		+	+		+	+	+	+
Stethojulis bandanensis	+	+	+			+	+	+
Thalassoma hardwicke								+
T. lutescens		+						+
T. purpureum								+
T. quinquevittantum								+
T. trilobatum						+		
Scarus brevifilis	+					+		
S. oviceps	+	+			+	+	+	+
S. psittacus	+	+				+	+	+
S. sordidus	+	+	+	+	+	+	+	+
Zanclus cornutus			+			+		+
Acanthurus lineatus		+	+		+			
A. mata	+	+	+	+			+	
A. nigricauda					+		+	
A. nigrofuscus		+			+	+	+	+
A. nigroris	+							
A. olivaceus			+		+		+	+
A. triostegus			+					
A. xanthopterus	+	+	+	+	+	+	+	+
Ctenochaetus striatus	+				+		+	
Naso lituratus	+	+					+	
N. unicornis	+	+		+	+	+	+	+
Zebrasoma scopas	+			+		+		
Z. veliferum					+			
Siganus spinus	+	+	+		+		+	+
Balistapus undulatus	+				+		+	+
Balistoides viridescens			+					
Rhinecanthus aculeatus		+	+	+			+	
Sufflamen bursa		+			+			
Ostracion cubicus	+				+			
O. meleagris	+	+	+	+	+	+	+	+
Canthigaster janthinoptera								+
C. solandri	+	+	+	+	+	+	+	+
C. valentini					+		+	
Diodon hystrix	+							
Species richness	51	47	40	28	41	37	44	47

Table 2. Coral species recorded at the eight stations in Papeete harbour.

Species	Stations							
	F1	F2	F3	F4	F5	F6	F7	F8
Scleractinia								
Psammocora contigua	+							+
P. profundacella		+	+		+	+		+
Stylocoeniella armata						+		
Pocillopora damicornis	+	+	+	+	+	+	+	+
P. verrucosa	+	+	+		+	+	+	+
Acropora valida	+	+		+		+	+	+
A. sp.				+		+		
Montipora spumosa	+			+	+		+	+
Montipora sp.			+			+		
Pavona cactus	+			+	+	+	+	
P. varians				+	+			
Fungia concinna			+			+	+	+
Herpolitha limax							+	
Porites rus	+	+	+	+	+	+	+	+
P. lutea	+	+	+	+	+		+	+
P. lobata	+					+		
Montastrea curta						+		+
Leptastrea transversa	+	+	+		+		+	+
Cyphastrea microphthalma							+	+
Acanthastrea echinata	+							
Lobophyllia hemprichii	+							
Zoanthidea								
Palythoa sp.	+	+					+	+
Corallimorpharia								
Rhodactis sp.	+			+		+	+	+
Milleporina								
Millepora platyphylla	+							
Species richness	15	8	8	9	9	13	13	14

Table 3. Hydrological characters of surface water measured at eight stations in the area of Papeete harbor. Values represent mean of annual surveys made from 1990 to 1995. Standard deviation in italics. Range (maximal and minimal values) in brackets.

	Stations							
	F1	F2	F3	F4	F5	F6	F7	F8
Temperature (°C)	28.42 *0.61* (27.8-29.0)	28.12 *0.63* (27.5-29.0)	28.45 *0.96* (28.0-29.2)	28.70 *1.01* (27.8-30.0)	28.25 *0.50* (28.0-29.0)	28.32 *0.47* (28.0-29.0)	28.15 *0.62* (27.5-29.0)	28.27 *0.26* (28.0-28.5)
Salinity (psu)	34.72 *1.27* (33.8-35.6)	31.97 *1.26* (29.7-34.3)	28.34 *0.04* (22.4-34.3)	34.50 *0.86* (33.9-35.1)	35.54 *0.19* (34.4-34.7)	35.09 *0.31* (34.9-35.3)	30.09 *1.05* (25.1-35.1)	35.04 *0.13* (34.9-35.1)
pH	8.12 *0.21* (7.8-8.2)	8.15 *0.17* (7.9-8.3)	8.17 *0.37* (7.8-8.5)	8.17 *0.31* (7.7-8.4)	7.96 *0.57* (7.1-8.3)	8.14 *0.29* (7.7-8.3)	7.98 *0.32* (7.5-8.2)	8.11 *0.34* (7.6-8.3)
Suspended matter ($mg.l^{-1}$)	4.19 *2.53* (1.6-6.7)	3.37 *2.55* (1.0-6.7)	3.20 *1.66* (1.9-5.6)	3.10 *0.66* (2.5-3.7)	1.91 *1.81* (0.4-4.5)	4.01 *2.83* (1.4-7.8)	3.48 *1.12* (2.3-3.3)	2.27 *0.98* (1.0-3.3)
Dissolved oxygen (ppm)	6.40 *0.55* (5.9-7.0)	6.60 *0.70* (6.1-7.4)	7.20 *0.50* (6.2-8.4)	6.70 *1.55* (5.8-8.5)	6.97 *1.77* (5.7-9.0)	6.88 *1.31* (6.0-8.4)	6.53 *1.69* (5.1-8.4)	6.87 *1.36* (5.8-8.4)
NH_4 ($\mu mol.l^{-1}$)	0.98 *1.17* (0.1-2.3)	1.12 *0.12* (1.0-1.2)	28.21 *5.13* (17.1-50.0)	1.18 *0.67* (0.8-2.0)	2.25 *0.72* (1.5-3.0)	1.20 *0.70* (0.4-1.8)	3.38 *1.06* (2.7-4.6)	1.33 *0.63* (0.6-1.8)
NO_2 ($\mu mol.l^{-1}$)	0.49 *0.52* (0.1-1.2)	0.51 *0.67* (0.1-1.5)	0.84 *0.67* (0.3-2.1)	0.55 *0.83* (0.1-1.8)	0.25 *0.19* (0.1-0.5)	0.35 *0.50* (0.1-1.1)	0.61 *0.86* (0.1-1.9)	0.35 *0.50* (0.1-1.1)
NO_3 ($\mu mol.l^{-1}$)	1.32 *1.70* (0.0-3.8)	1.37 *1.09* (0.6-2.1)	1.82 *0.42* (1.2-3.0)	0.66 *0.59* (0.1-1.2)	1.61 *0.63* (1.1-2.5)	1.51 *1.07* (0.7-3.1)	1.19 *0.83* (0.1-2.1)	2.47 *2.62* (0.8-6.4)
PO_4 ($\mu mol.l^{-1}$)	0.79 *1.20* (0.1-2.6)	1.94 *3.08* (0.1-5.5)	1.51 *3.11* (1.1-2.0)	0.50 *0.43* (0.3-1.0)	0.38 *0.54* (0.1-1.2)	0.31 *0.33* (0.1-0.8)	2.32 *3.52* (0.5-7.6)	0.34 *0.52* (0.1-1.2)
SiO_2 ($\mu mol.l^{-1}$)	20.52 *20.25* (1.6-51.5)	8.95 *7.10* (1.3-18.0)	30.69 *5.12* (2.1-98.6)	3.60 *2.59* (0.6-6.0)	6.77 *4.97* (1.4-11.2)	2.06 *1.70* (0.5-2.6)	28.20 *27.99* (2.3-67.4)	7.86 *9.98* (0.5-22.5)
Fe ($\mu g.l^{-1}$)	21.85 *10.73* (6.5-30.9)	86.00 *54.25* (39.0-150.0)	101.00 *47.48* (61.0-165.0)	47.75 *31.74* (19.0-93.0)	21.25 *12.12* (13.0-39.0)	25.25 *18.78* (12.0-53.0)	133.25 *85.13* (29.0-237.0)	30.75 *28.93* (1.0-62.0)
Cu ($\mu g.l^{-1}$)	1.57 *1.50* (0.5-3.8)	1.87 *1.03* (1.0-3.0)	1.90 *0.63* (1.2-2.4)	1.70 *0.47* (1.0-2.0)	1.30 *0.60* (1.0-2.2)	0.85 *0.19* (0.6-1.0)	1.65 *0.66* (1.0-2.4)	1.15 *0.92* (0.5-2.5)
Zn ($\mu g.l^{-1}$)	7.52 *5.23* (3.6-15.2)	15.82 *21.04* (2.0-47.0)	5.51 *10.02* (2.3-14.8)	13.65 *13.29* (2.0-31.0)	10.25 *3.78* (6.7-14.0)	10.90 *8.41* (2.8-22.0)	23.12 *24.95* (4.8-60.0)	6.72 *7.95* (0.2-17.9)

ATOLL RESEARCH BULLETIN

NO. 485

COLONIZATION OF THE F/V *CALÉDONIE TOHO 2* WRECK BY A REEF-FISH ASSEMBLAGE NEAR NOUMÉA (NEW CALEDONIA)

BY

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ISSUED BY
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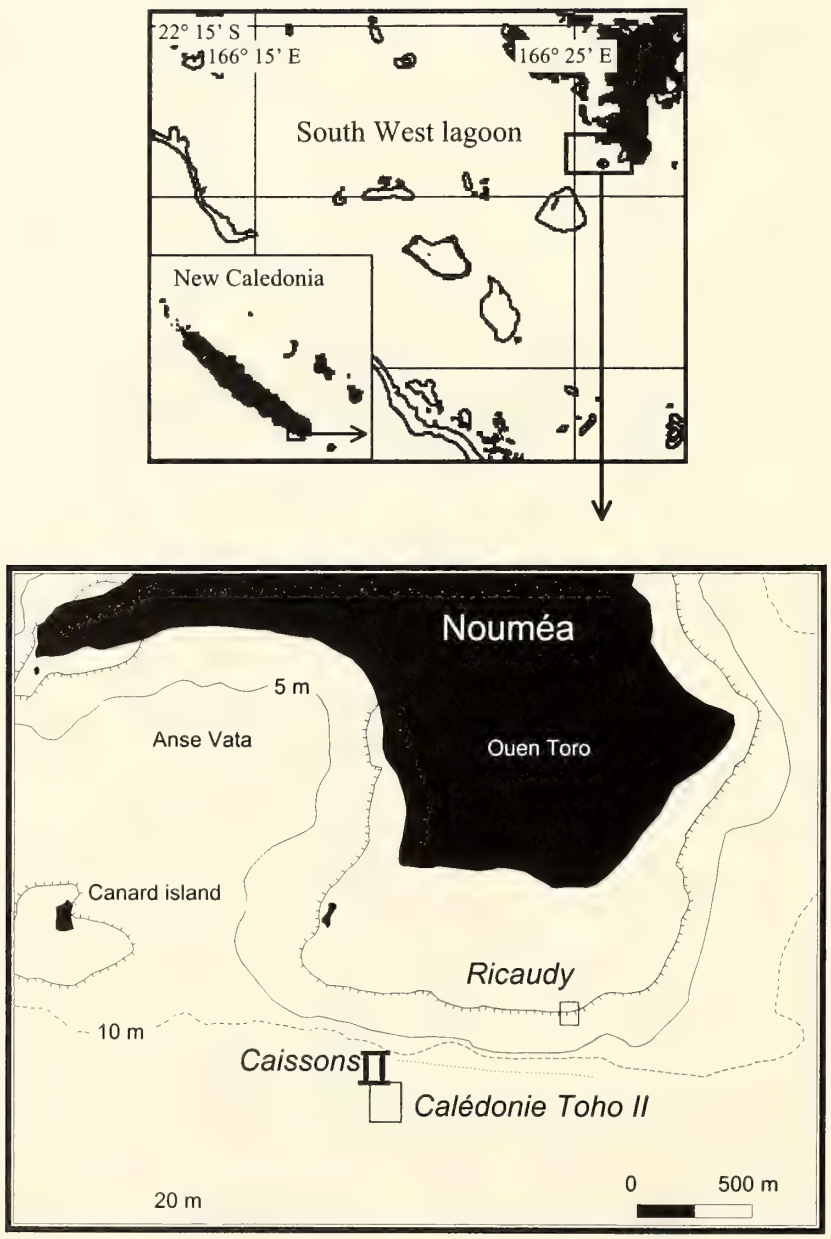

Figure 1. Location of the study area.

COLONIZATION OF THE *F/V CALÉDONIE TOHO 2* WRECK BY A REEF-FISH ASSEMBLAGE NEAR NOUMÉA (NEW CALEDONIA)

BY

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ABSTRACT

The colonization of the *F/V Calédonie Toho 2* was studied for a period of 13 months after the ship was scuttled. A nearby assemblage of US Marine floating bridge boxes (*Caissons*) sunk during WWII and a natural fringing reef (*Ricaudy*) were surveyed at the same time. Species richness on the *Calédonie Toho 2* increased to reach 42 species 398 days after scuttling. Fish density increased for 109 days after scuttling to reach a mean of 8.15 fish/m^2, with exceptional peaks during recruitment phases. Fish biomass increased in two steps to reach an average of 336 g/m^2 193 days after scuttling. The number of common species was higher between the *Calédonie Toho 2* and the *Caissons* (54 species) than *Calédonie Toho 2* and *Ricaudy* (20 species). *Ricaudy* fish assemblages were characterized by species associated with live corals whereas the artificial reefs were characterized by pelagic and opportunist species. Differences occurred between the *Calédonie Toho 2* assemblage, characterized by numerous sciophylous species (Apogonidae), and the *Caissons* assemblage, characterized by large carnivorous species (Serranidae, Lutjanidae). These differences were due to the different size, shape and age of the two artificial reefs. The *Calédonie Toho 2* assemblage evolved from a pioneer to a "secondary" assemblage, with four species assemblages being successively identified. The first step of the colonization was the arrival of large fish from the *Caissons* and the recruitment of *Chromis fumea* (Pomacentridae). The other species assemblages were characterized by seasonal recruitment of juveniles and migration of pelagic and opportunist adult fish species. The "secondary" assemblage was characterized by an increasing migration of adults of specialized benthic species despite the persistence of a pool of pelagic and opportunist species. Consequently, the *Calédonie Toho 2* acted more as an attraction device located on bare sand than a productive structure for the surrounding environment during the first 13 months after the scuttling.

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INTRODUCTION

Artificial reefs have been widely used in the marine environment to enhance fishing yields because of their capacity to attract and aggregate fish. However, this use may accelerate the decline of heavily exploited fish stocks by concentrating fish and fishing efforts into a restricted area, rather than contributing to enhance fish production through growth, reproduction and survival processes. This attraction-production debate has been widely discussed (among others, Bohnsack, 1989; Chou et al., 1992; Bohnsack, 1996; Carr and Hixon, 1997; Grossman et al., 1997; Pickering and Whitmarsh, 1997). Each case is different because numerous factors are involved such as reef design, reef location, fishing effort and management policy (Chou et al., 1992; Brock, 1994; Bohnsack, 1996; Chou, 1997). Currently, man-made reefs are used as a management tool to compensate for overfishing and anthropogenic degradation (Grove, 1982; Chou et al., 1992; Bohnsack et al., 1997; Chou, 1997). They provide new habitats for juveniles and adults, and contribute to protecting resources if fishing is restricted around the artificial reef (Bohnsack, 1989; Chou, 1997; Grossman et al., 1997). If artificial reefs are located in the coastal zone for mitigation purposes, they can induce economic benefits other than fishing when used for ecotourism and scuba diving. This may be the most economically viable use of an artificial reef (Brock, 1994).

In New Caledonia, artificial reefs located in the lagoon have several origins. There are several shipwrecked vessels generally located near natural reefs, remains of US military equipment from World War II (*Caissons*) sunk in the lagoon near Nouméa, and two vessels recently sunk by local authorities for scuba diving purposes. In 1996, the Service de la Mer de la Province Sud had the opportunity to sink a third vessel, *F/V Calédonie Toho 2*. The ship was sunk to create a scuba diving site near Nouméa where tourism activity is concentrated.

After the scuttling of the ship, the Service de la Mer de la Province Sud funded a scientific survey in order to study the colonization of the wreck by a fish assemblage. The different steps of the colonization process and the identification of ecological changes were analyzed. Species similarity on a nearby artificial reef (*Caissons*) and the closest natural reef (*Ricaudy*) was assessed. This study of the colonization by a fish assemblage contributes to the understanding of the attraction-production debate. The proximity of the *Caissons* allowed quantifying the interactions between the new artificial reef and the surrounding communities. The results are of particular interest in the coral reef environment because of a lack of scientific data (Carr and Hixon, 1997). Moreover, most artificial reefs studied are quarry rocks, concrete blocks, old tires and oil production platforms but shipwrecks have seldom been studied.

MATERIAL AND METHODS

The *F/V Calédonie Toho 2* (CT2) was a Japanese long-liner (length 44.7 m, width 7.6 m and height 15 m including upper works) of 121-ton burden (one-ton burden represents a weight of 1,000 kg and a volume of 1 m^3). The ship was sunk August 9, 1996 near Nouméa (Fig. 1). It lies on its starboard, at a depth of between 20 and 23 m, on a muddy sand substrate with scarce epibenthic organisms: alcyonarians

(*Spongodes merleti*); holothurians (*Actinopyga echinites*); and sea stars (*Protoreaster nodosus*). A few bioclasts, which are colonized by sponges, hydroids, nudibranchs or feather stars (*Himerometra robustipinna*), are present on the sea floor. This type of biotope was identified as "silted bottoms under terrigenous influence" by Richer de Forges et al. (1987). The visibility varied between 5 and 10 m and the main currents were directed from the hull to the deck. Consequently, currents were weak on the deck side of the boat. By the end of the survey, the CT2 was colonized by 22 benthic taxa (algae, sponges, corals, anthozoa, mollusks, crustaceans, echinoderms and sea squirts).

The *Caissons* are made of an assemblage (19 x 19 m, maximum pile height 6 m) of 30 iron US Marine floating bridge boxes (2 m side) sunk between 1942 and 1945. They are located between 17 and 20 m depth in the same biotope as the CT2 (Fig. 1). The nearest box is located 7 m from the stern of the wreck. The boxes, sunk more than 50 years ago, are heavily corroded and colonized by 29 typical hard-bottom benthic flora and fauna taxa (algae, sponges, corals, alcyonarians, anthozoa, mollusks, crustaceans, echinoderms and sea squirts).

The closest natural reef formation, *Ricaudy* fringing reef (Fig. 1), 280 m away from the CT2 and between 1 and 3 m depth, is characterized by a windward outer slope with live corals, mainly branching *Acropora* spp., *Pocillopora* spp., Poritidae and Favidae. The reef flat is characterized by rubble in the upper parts and algae beds (*Sargassum* sp. and *Turbinaria ornata*) in the deeper parts. This reef was used as a reference station.

Census of Fish

The fish assemblages of the three sites (CT2, *Caissons* and *Ricaudy*) were regularly sampled during the 13 months following the scuttling of the boat (Table 1). Sampling frequency was higher at the beginning of the survey in order to identify initial fish colonization accurately. The stations were sampled once a week during the first two months, once every two weeks during the following two months, and once a month during the last nine months. The frequency was occasionally modified because of bad weather conditions (hurricane, tropical depression), mainly for *Ricaudy* as this station is inaccessible in high wind. Unfortunately, the *Caissons* fish community was not censused before the blast of the CT2 because the survey was funded after the scuttling. However, qualitative and semi-quantitative observations were made by Chauvet (pers. com.) on the effect of the blast on the *Caissons* fish community. These observations were made on the sea surface and the sea floor just after the blast.

The fish assemblages of the CT2 and the *Caissons* were censused by visual counts (time for each census ranged from 45 to 60 minutes). All fish located inside the structures and in a 5 m perimeter around the artificial reefs were identified and counted by two divers, each diver sampling different fish families. The divers estimated the fork length of the fish. Fish weights were calculated from length-weight relationships (Kulbicki et al., 1993; 1994). The surface areas sampled were 1,067 m^2 for the CT2 and 856 m^2 for the *Caissons*.

Table 1. Sampling calendar of the *Calédonie Toho 2*, the *Caissons* and *Ricaudy* reef.

Date	N°	Days	Calédonie Toho 2	Caissons	Ricaudy
20 08 1996	1	11	x	x	x
26 08 1996	2	17	x	x	-
02 09 1996	3	24	x	x	x
09 09 1996	4	31	x	x	-
17 09 1996	5	39	x	x	-
01 10 1996	6	53	x	x	x
15 10 1996	7	67	x	x	x
28 10 1996	8	80	x	x	x
26 11 1996	9	109	x	x	x
09 12 1996	10	122	x	x	x
18 02 1997	11	182	x	x	x
18 03 1997	12	210	x	x	-
11 04 1997	13	234	x	x	x
16 05 1997	14	269	x	x	-
09 06 1997	15	293	x	x	x
18 07 1997	16	332	x	x	x
08 08 1997	17	353	x	x	x
11 09 1997	18	387	x	x	x

N° = sample number; Days = number of days after the scuttling of the *Calédonie Toho 2*; x = sampling completed; - = no sampling.

Distance sampling (Burnham et al., 1980; Buckland et al., 1993) was used to sample the *Ricaudy* fish community. A 50-m line transect was laid on the sea floor. All fish along the transect were identified and counted by the same divers who sampled the artificial reefs. The fork lengths and perpendicular distances of the fish to the transect were estimated. Fish which were more than 10 m from the transect were not recorded.

The divers had a good knowledge of the fish fauna and previous training in visual censuses. Previous works show that differences in length, distance and number estimates are likely to be minor (Wantiez et al., 1997; Kulbicki and Sarramégna, 1999).

Data Analysis

Fish densities and biomasses on the CT2 and the *Caissons* were calculated by dividing numbers and weights of fish by surface areas. On *Ricaudy*, densities and biomass were calculated by the average distances method (Kulbicki and Sarramégna, 1999), i.e.:

$$De = (2L)^{-1}\sum_{i=1}^{p} n_i d_i^{-1} \text{ and } Bi = (2L)^{-1}\sum_{i=1}^{p} w_i d_i^{-1},$$

where De = density (fish/m^2), L = transect length (50 m), n_i = abundance of species i, d_i = average distance for species i to the transect (m), p = number of species,

Bi = biomass (g/m^2), and w_i = weight of species i (g). Average distance for species i to the transect is calculated as follows:

$$d_i = \frac{1}{n_i} \sum_{j=1}^{o_i} n_j d_j,$$

where o_i = number of occurrences of species i, n_j = number of fish of species i observed at occurrence j, and d_j = distance of fishes i to the transect at occurrence j. These estimations are easy to calculate and yielded values very close to the best fits using complicated algorithms (Kulbicki and Sarramégna, 1999).

Correspondence analysis (Legendre and Legendre, 1984) was used to study the fish assemblage structures of the three sites and to analyze fish colonization of the CT2. This analysis was performed on the data matrix of the density of the species. No data transformations were necessary to clarify the projections of the objects (samples) and descriptors (species) or to identify the different structures and their characteristic species assemblages.

RESULTS

Effects of the Blast

The blast of the CT2 induced some fish mortality in a 40 m perimeter around the boat. The soft-bottom fish community was little affected. Less than 50 specimens of *Lethrinus genivittatus* and *Nemipterus peronii* were killed. The *Caissons* fish community was also affected. The highest mortality affected *Priacanthus hamrur* (around 400 kg). Two other species were significantly affected: *Lutjanus argentimaculatus* and *Lutjanus russelli* (less than 25 kg). The rest of the large species were seldom affected. In particular, no dead Carangidae and Serranidae were censused.

Temporal Variations

A total of 183 fish species was recorded during this survey. Seventy eight species (29 families) were censused on the CT2 with Carangidae (9 species), Pomacentridae (9 species), Apogonidae (8 species) and Lutjanidae (8 species) being the most diversified families. Eighty eight species (30 families) were censused on the *Caissons* with Pomacentridae (11 species), Carangidae (10 species) and Serranidae (9 species) being the most diversified families. One hundred species (23 families) were censused on *Ricaudy* with Labridae (20 species), Pomacentridae (19 species) and Chaetodontidae (15 species) being the most diversified families. Species richness on the CT2 increased throughout the survey (Fig. 2) from 5 species, 11 days after scuttling, to a maximum of 42 species, 398 days after scuttling. Species colonization was most significant during the first 20 days, with the first colonization step involving pioneer species. After that, species richness increased regularly to reach a level of 31-35 species after 221 days.

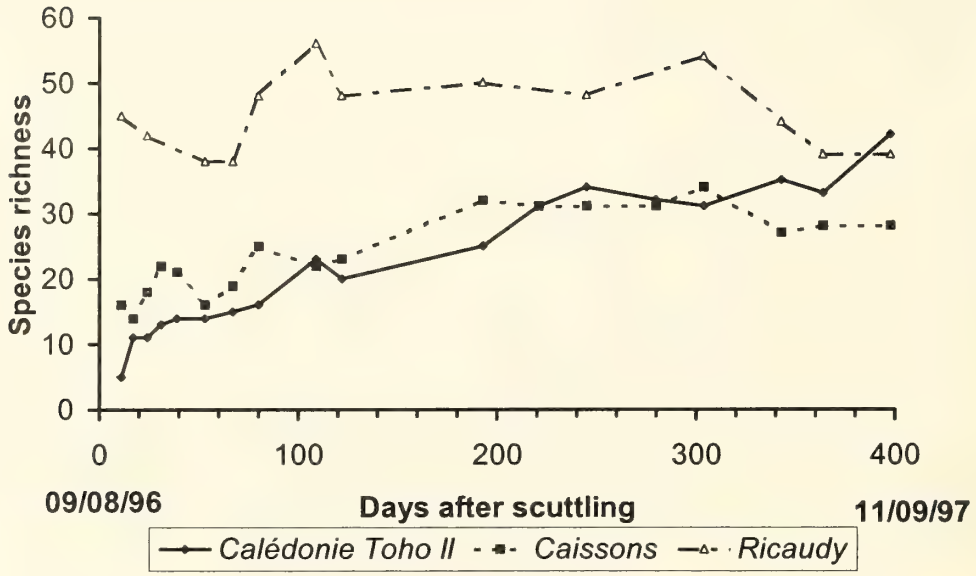

Figure 2. Temporal variations of fish species richness on *Calédonie Toho 2*, *Caissons* and *Ricaudy* reef.

A new increase phase was observed during the final sampling. These species will be referred to as "secondary" species. On the *Caissons*, species richness increased overall during the first 193 days from 16 to 32 species (Fig. 2). After this colonization phase, species richness remained relatively stable at approximately between 28 and 34 species during the rest of the survey. Variations of species richness on the natural reef (*Ricaudy*) were relatively low (Fig. 2). On average, 45 species were recorded during the survey. Species richness was lower in winter (40 species on average), from September to October 1996 (11 to 67 days after scuttling) and from July to mid-September 1997 (343 to 398 days after scuttling). Species richness was higher during the rest of the year (50 species on average). During the survey, species richness was significantly higher on *Ricaudy* than on both artificial reefs (χ^2 proportionality test, $P < 0.05$), with differences between CT2 and *Caissons* not being significant (χ^2 proportionality test, $P > 0.05$).

Fish density increased rapidly during the first 109 days after scuttling (Fig. 3). This increase was mainly due to the settlement of planktivorous schooling species (Clupeidae, Apogonidae and Pomacentridae) and the migration of carnivorous species (Carangidae, Lutjanidae). After this increase, density remained relatively stable (around 8.15 fish/m^2) with the exceptional peaks occurring between 304 and 364 days after scuttling. These high values corresponded to the recruitment of Apogonidae, *Rhabdamia* spp. The density of these species decreased dramatically in the last sample because recruitment had ended and because of predation. The schools of Carangidae were feeding on small fish, which ventured out of their shelters (upper works or holds). On the *Caissons*, density increased for 67 days following scuttling (Fig. 3) due to the recruitment of the same small species as on the CT2 and the presence of the same species of Carangidae. The density remained relatively stable between 67 and 193 days, then decreased to an average of 1.32 fish/m^2. This second level was due to

the end of the recruitment of Clupeidae (*Spratelloides* spp.) while predation by Carangidae persisted. On *Ricaudy*, density remained relatively stable throughout the survey (Fig. 3) with fish population being dominated by parrotfish juveniles (*Scarus* spp.) and adult Pomacentridae (*Abudefduf sexfasciatus*, *Pomacentrus molluccensis* and *Stegastes nigricans*). At the end of the survey, fish density was highest on the CT2 because of the presence of schools of Apogonidae and juveniles, while densities were comparable on *Caissons* and *Ricaudy* (Fig. 3).

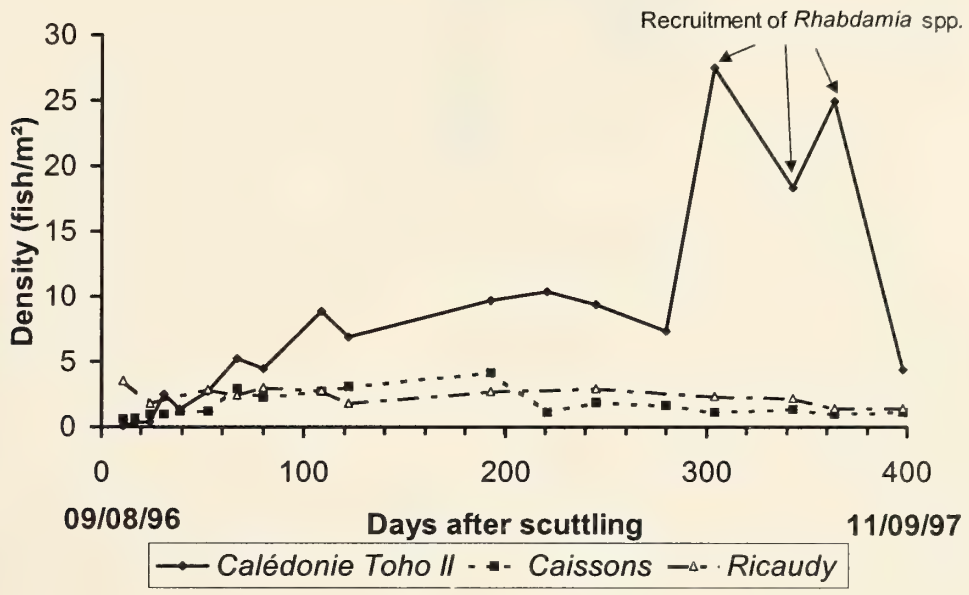

Figure 3. Temporal variations of fish density on *Calédonie Toho 2*, *Caissons* and *Ricaudy* reef.

Fish biomass on the CT2 increased during the 53 days after scuttling (Fig. 4). This increase was mainly due to the migration of *Lutjanus russelli* from the *Caissons*. The biomass stabilized at an average of 153 g/m^2 between 53 and 193 days after scuttling. Important variations were observed after this first colonization phase, due to the occasional presence of Carangidae (unidentified Carangidae and *Carangoides dinema*), large *Lutjanus argentimaculatus* and Sphyraenidae (*Sphyraena flavicauda* and *Sphyraena jello*). At the end of the survey, biomass reached an average of 336 g/m^2. The largest fish recorded were rays (*Taeniura melanospila*) of more than 200 kg and five groupers (*Epinephelus coioides*) from 0.5 kg to 13 kg, the first specimens being recorded 11 days after scuttling. On the *Caissons*, mean biomass remained relatively stable (174.3 g/m^2) despite important variations (Fig. 4). With two exceptions (24 and 304 days after scuttling), a school of *Lutjanus russelli* constituted more than 45% of the overall biomass. Biomass variations were mainly related to the fluctuation in size of this school. On *Ricaudy*, biomass remained stable (52.2 g/m^2 on average) during the survey (Fig. 4). At the end of the survey, fish biomass was higher on CT2 and lower on *Ricaudy*.

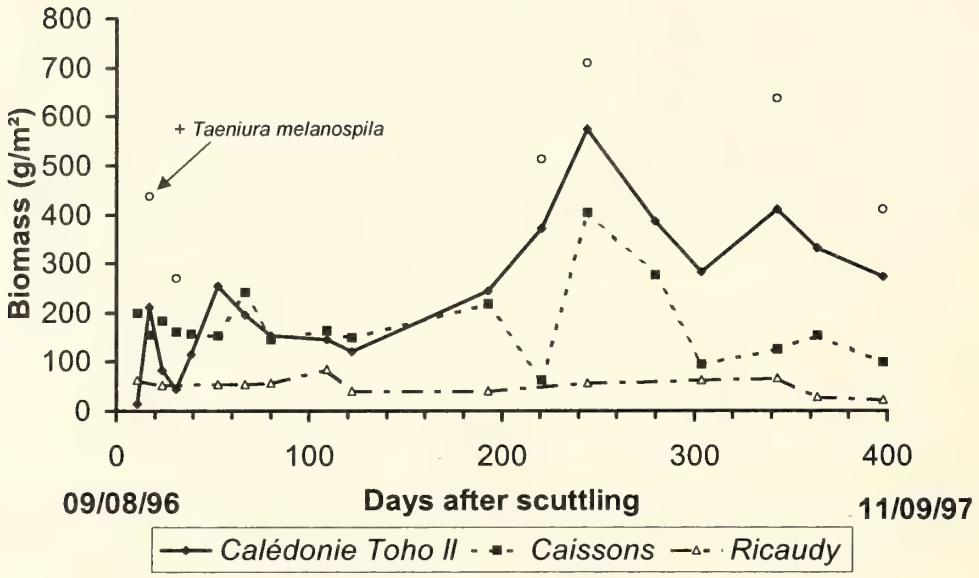

Figure 4. Temporal variations of fish biomass on *Calédonie Toho 2*, *Caissons* and *Ricaudy* reef.

Species Similarity and Fish Assemblages

Fish species were more similar between the CT2 and the *Caissons* than between the two artificial reefs and *Ricaudy* (Fig. 5). Artificial reefs shared 54 species (69.2% of the species recorded on the CT2). On the other hand, only 20 species were censused on both the CT2 and *Ricaudy* (25.6% of the species recorded on the CT2). Only 14 of these species were present on all three sites, mainly planktivores (Clupeidae, Apogonidae and Pomacentridae), macro-carnivorous species (*Plectropomus leopardus*, *Lethrinus lentjan*) and two micro-herbivorous species (*Scarus ghobban* and *Acanthurus blochii*). The number of species in common between the CT2 and the *Caissons* increased during the 245 days after scuttling to reach 22 (Fig. 6). Two groups of species were involved. The first group consisted of species coming from the *Caissons*, which migrated to the wreck. The second group consisted of adult lagoon species, which colonized the two artificial reefs, and juveniles, which simultaneously colonized the two structures. After this phase, the number of species recorded on both artificial reefs remained around 20 with variations linked to the occasional presence of pelagic and opportunist species. The number of species in common between the CT2 and *Ricaudy* increased very slowly (Fig. 6). An average of five species (maximum six species) was seen simultaneously on the two sites.

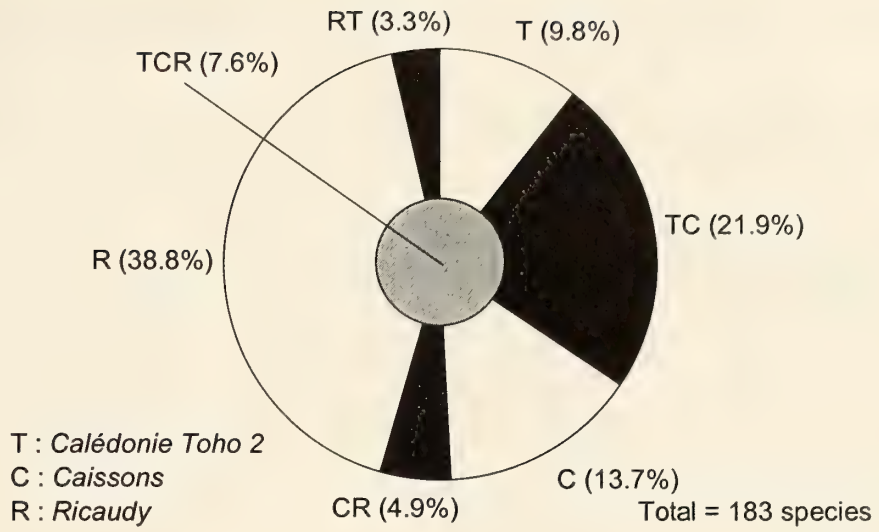

Figure 5. Species similarity among *Calédonie Toho 2*, *Caissons* and *Ricaudy* reef assemblages.

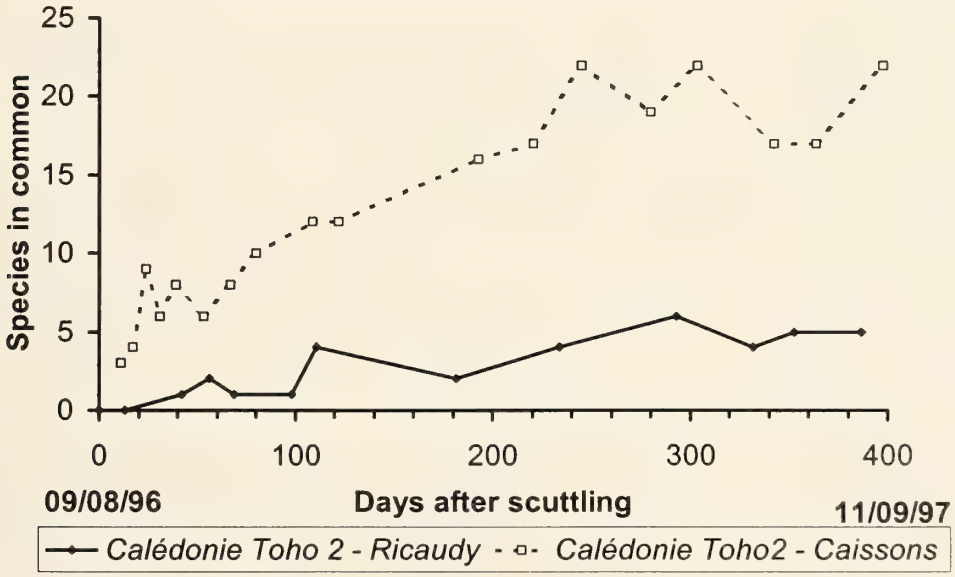

Figure 6. Temporal variations of species similarity between *Calédonie Toho 2*, *Caissons* and *Ricaudy* reef.

Correspondence analysis showed that the fish assemblage structures of the artificial reefs (CT2 and *Caissons*) were different from that of *Ricaudy* reef (Fig. 7). *Ricaudy* fish assemblage was characterized by species with a high coral reef affinity (Table 2): Chaetodontidae (*Chaetodon* spp.), Pomacentridae (*Abudefduf* spp., *Chromis* spp., *Stegastes nigricans*), Labridae (*Halichoeres* spp., *Thalassoma* spp.) and Scaridae (*Scarus* spp.). The artificial reefs were characterized by pelagic species (Clupeidae, Carangidae, Sphyraenidae, *Scomberomorus commerson*), lagoon opportunist species (Lutjanidae, Lethrinidae), large Serranidae, one Caesionidae (*Pterocaesio marri*), one

Priacanthidae (*Priancanthus hamrur*), and recruits of Pomacentridae and Apogonidae (Table 3).

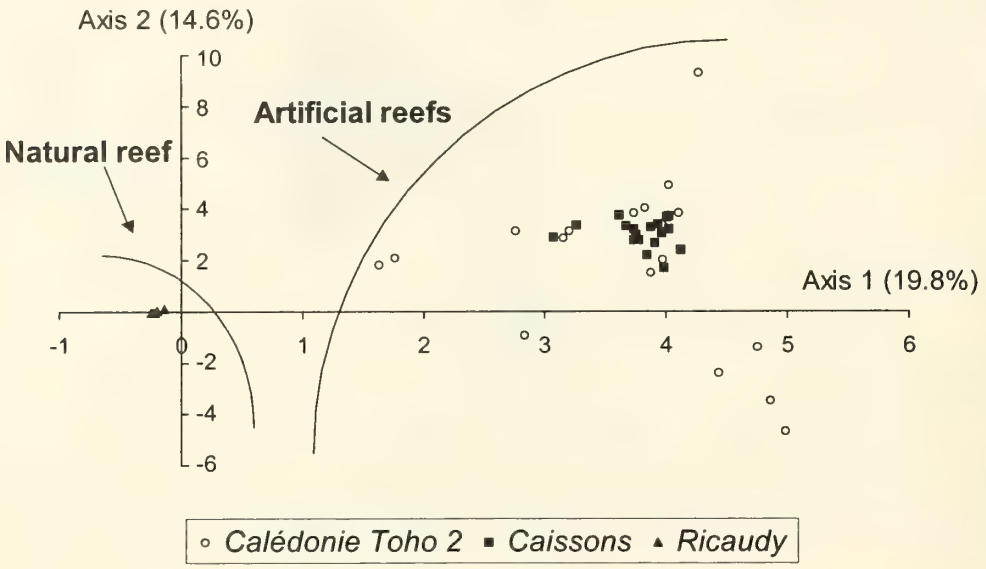

Figure 7. Correspondence analysis of the community structure (projection of the samples) of *Calédonie Toho 2*, *Caissons* and *Ricaudy* fish assemblages. The percentage of the total variance explained by the axes are given.

The fish assemblages of the CT2 and the *Caissons* displayed numerous similarities (Fig. 7). Differences concerned the Apogonidae that recruited on the wreck and the presence of several large Serranidae and Lutjanidae on the *Caissons* (Table 3). Fish community structure of the *Caissons* remained relatively stable during the study, whereas ecological changes affected the CT2 fish community (Fig. 7).

Ecological Changes

Ecological changes were identified by the correspondence analysis performed on the fish assemblages of the CT2 (Fig. 8). A pioneer assemblage was observed during the first 221 days after scuttling (samples 1 to 12; Fig 8). The recruitment of juveniles and the migration of adults from the *Caissons* or the surrounding lagoon characterized this phase. Three steps were identified during the first 193 days (samples 1 to 11; Fig. 8). During the first 31 days (samples 1 to 4), large adult fish (Serranidae and Carangidae) coming from the *Caissons* and recruits of one species of Pomacentridae (*Chromis fumea*) colonized the wreck (Table 3). The second step took place between 39 and 109 days (samples 5 to 9; Fig. 8). The fish assemblage structure was modified by a massive recruitment of juveniles, mainly Clupeidae, Apogonidae and unidentified Pomacentridae (Table 3). Adults of new pelagic and opportunist species were also censused during this period (Dasyatidae and Carangidae). The third step occurred between 122 and 193 days after scuttling (samples 10 and 11; Fig. 8). During this period, new pelagic species were censused (Carangidae) and one species of Pseudochromidae and one of Scaridae migrated on to wreck (Table 3). In sample n° 12 (221 days after scuttling) the characteristic species of the third step were not censused.

Consequently, this sample displayed similarities with the fish assemblage censused during the second step of this pioneer colonization phase (Fig. 8).

Table 2. Characteristic species of the fish assemblage of *Ricaudy* reef, determined by the correspondence analysis.

Ricaudy		
Tylosurus crocodilus	*Chaetodon trifascialis*	*Halichoeres hortulanus*
Sargocentron sp	*Chaetodon ulietensis*	*Halichoeres margaritaceus*
Fistularia commerson	*Chaetodon unimaculatus*	*Hemigymnus melapterus*
Synanceia verrucosa	*Chaetodon vagabundus*	*Labroides dimidiatus*
Epinephelus caeruleopunctatus	*Abudefduf septemfasciatus*	*Stethojulis strigiventer*
Epinephelus macrospilos	*Abudefduf sexfasciatus*	*Thalassoma hardwicke*
Epinephelus merra	*Abudefduf vaigiensis*	*Thalassoma jansenii*
Plectropomus leopardus	*Abudefduf whitleyi*	*Thalassoma lunare*
Apogon aureus	*Amphiprion melanopus*	*Thalassoma lutescens*
Apogon fuscus	*Chromis agilis*	*Thalassoma trilobatum*
Cheilodipterus quinquelineatus	*Chromis viridis*	*Chlorurus sordidus*
Trachinotus blochii	*Chromis chrysura*	*Scarus* sp
Lutjanus fulviflamma	*Chromis* sp	*Scarus altipinnis*
Lethrinus harak	*Chrysiptera taupou*	*Scarus rivulatus*
Lethrinus lentjan	*Neopomacentrus violascens*	*Scarus ghobban*
Lethrinus atkinsoni	*Neoglyphidodon melas*	*Scarus schlegeli*
Lethrinus obsoletus	*Neoglyphidodon polyacanthus*	Blenniidae spp
Scolopsis bilineatus	*Plectroglyphidodon leucozonus*	*Acanthurus blochii*
Scolopsis trilineatus	*Pomacentrus bankanensis*	*Acanthurus triostegus*
Parupeneus ciliatus	*Pomacentrus moluccensis*	*Ctenochaetus striatus*
Parupeneus indicus	*Pomacentrus* sp	*Zebrasoma scopas*
Parupeneus multifasciatus	*Pomacentrus vaiuli*	*Zebrasoma veliferum*
Chaetodon auriga	*Stegastes nigricans*	*Siganus argenteus*
Chaetodon bennetti	Labridae sp2	*Siganus corallinus*
Chaetodon citrinellus	Labridae sp3	*Siganus doliatus*
Chaetodon ephippium	Labridae spp	*Siganus puellus*
Chaetodon flavirostris	*Cheilinus chlorourus*	*Siganus punctatus*
Chaetodon lineolatus	*Cheilinus trilobatus*	*Siganus spinus*
Chaetodon lunula	*Cheilio inermis*	*Euthynnus affinis*
Chaetodon lunulatus[1]	*Choerodon fasciatus*	*Oxymonacanthus longirostris*
Chaetodon melannotus	*Choerodon graphicus*	*Arothron hispidus*
Chaetodon plebeius	*Gomphosus varius*	*Arothron manillensis*
Chaetodon speculum	*Halichoeres argus*	

[1]: sister species of the Indian Ocean species *Chaetodon trifasciatus*

Table 3. Characteristic species of the fish assemblages of the *Calédonie Toho 2* and the *Caissons*.

Characteristic species of the *Calédonie Toho 2* and the *Caissons*		
Cephalopholis urodeta	*Symphorus nematophorus*	*Neopomacentrus* sp1
Epinephelus cyanopodus	*Pterocaesio marri*	*Pomacentrus imitator*
Priacanthus hamrur	*Lethrinus* sp	*Sphyraena jello*
Carangoides dinema	*Lethrinus nebulosus*	*Ecsenius midas*
Pseudocaranx dentex	*Kyphosus vaigensis*	*Meicanthus atrodorsalis*
Lutjanus adetii	*Chaetodon kleinii*	*Gobiidae* spp
Lutjanus argentimaculatus	*Centropyge bicolor*	*Lactoria cornuta*
Lutjanus fulvus	*Pomacanthus sextriatus*	*Arothron stellatus*
Lutjanus vitta		
Characteristic species of the *Calédonie Toho 2* only		
Pioneer assemblage (N° 1 to 12)		
Pterocaesio marri(2)		*Sphyraena jello* (2)
N°1 to 4 (◆)	N°5 to 9 and 12 (◇)	N°10 and 11 (▲)
Taeniura melanospila (2)	*Dasyatis kuhlii* (2)	*Caranx papuensis* (2)
Epinephelus coioides (2)	*Aetobatus narinari* (2)	*Trachinotus bailloni* (2)
Plectropomus leopardus (2)	*Spratelloides* sp (1)	*Pseudochromis paccagnellae* (1)
Caranx melampygus (2)	*Apogon doederleini* (1)	*Scarus rivulatus* (2)
Gnathanodon speciosus (2)	*Apogon fraenatus* (1)	
Lutjanus sp (2)	*Sillago* sp (2)	
Platax orbicularis (2)	*Echeneis naucrates* (2)	
Chromis fumea (1)	*Carangidae* spp (2)	
Bodianus perditio (1,2)	*Atule mate* (2)	
Acanthurus blochii (2)	*Caranx lugubris* (2)	
	Pomacentrus sp (1)	
	Scomberomorus commerson (2)	
	Arothron nigropunctatus (2)	
N° 13 (□)		
Apogon sp (1)	*Chrysiptera taupou* (1)	*Sphyraena flavicauda* (2)
Plectrorhinchus picus (1)		
Secondary assemblage (N° 14 to 18; ●)		
Pterois volitans (2)	*Parupeneus heptacanthus* (2)	*Labridae sp2* (2)
Epinephelus maculatus (2)	*Parupeneus multifasciatus* (2)	*Scarus ghobban* (2)
Apogon aureus (1)	*Chaetodon lineolatus* (2)	*Pterelеotris* sp (2)
Apogon fuscus (1)	*Coradion altivelis* (2)	*Siganus argenteus* (2)
Archamia fucata (1)	*Heniochus acuminatus* (2)	*Ostracion cubicus* (2)
Cheilodipterus quinquelineatus (1)	*Chrysiptera starcki* (1)	*Arothron manillensis* (2)
Rhabdamia sp (1)	*Neopomacentrus azysron* (1)	*Canthigaster bennetti* (1)
Aprion virescens (2)	*Pomacentrus coelestis* (1)	*Canthigaster valentini* (1)
Lutjanus kasmira (2)	*Sphyraena putnamiae* (2)	alevins indéterminés (1)
Lethrinus lentjan (2)		
Characteristic species of the *Caissons* only		
Gymnothorax javanicus	*Cephalopholis sonnerati*	*Selar crumenophthalmus*
Synodus dermatogenis	*Cephalopholis* sp	*Lutjanus fulviflamma*
Syngnathidae spp	*Epinephelus* sp	*Lutjanus russelli*
Cephalopholis boenack	*Caranx sexfasciatus*	*Diagramma pictum*
Cephalopholis miniata		

N° = sample number (Table 1); 1 = juveniles; 2 = adults. Symbols refer to Figure 8.

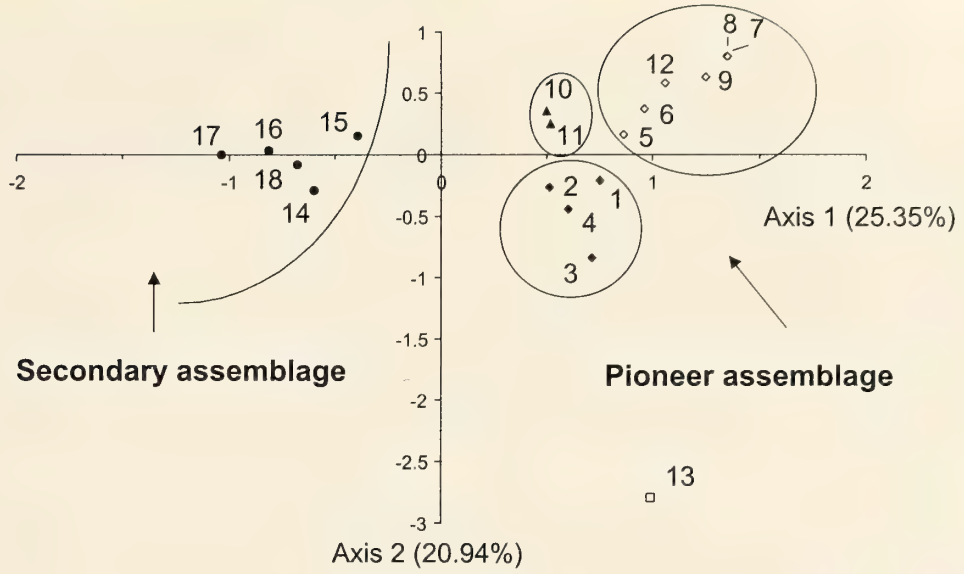

Figure 8. Correspondence analysis of the temporal variations of the community structure (projection of the samples) of *Calédonie Toho 2* fish assemblage. The percentage of the total variance explained by the axes are given. The numbers of the samples are in chronological order (see Table 1).

The fish assemblage structure was different 245 days after scuttling (sample 13; Fig. 8). This sample was characterized by the same species as in the pioneer assemblages and by the recruitment of Apogonidae and the migration of a school of Sphyraenidae from the lagoon (Table 3). This sample can be considered as a transitory assemblage from a pioneer assemblage to a more evolved one.

From 280 days after scuttling to the end of the survey (sample 14 to 18), the fish assemblage on the CT2 evolved to a "secondary" assemblage (Fig. 8). This phase was characterized by the recruitment of five species of Apogonidae and three species of Pomacentridae (Table 3). Adults of Scorpaenidae, Lutjanidae, Chaetodontidae, Scaridae, Siganidae, Ostraciidae and Tetraodontidae characterized this secondary assemblage (Table 3). Some of these secondary species were not censused on the *Caissons* (Scorpaenidae, Lutjanidae, Siganidae, Tetraodontidae).

DISCUSSION

Natural Variations

Temporal variations of species richness, density and biomass on *Ricaudy* reef were typical of fringing reefs in New Caledonia (Kulbicki, 1991), Tahiti (Galzin, 1985) and La Réunion (Letourneur and Chabanet, 1994). These variations are linked to natural processes such as recruitment patterns during summer (Molina, 1982; Galzin, 1985; Letourneur and Chabanet, 1994; Caley, 1995). Consequently, no particular event occurred during this study.

Temporal Variations

The colonization of the CT2 by a fish assemblage was characterized by a rapid increase in species richness, density and biomass because of the proximity of the *Caissons*. Migration of adult fish to the CT2 contributed to the colonization of the ship. Although rapid colonization of artificial reefs by fish has been well documented (Bohnsack et al., 1994; Cummings, 1994), no study on the colonization of a similar artificial reef (type, size, shape and habitat location) was available. Carr and Hixon (1997) studied fish colonization on small structures (4 m^2). They reported an increase of species richness during the first 210 days after the start of their survey, as in the present study. However, because of the size of the CT2, it is likely that further colonization of new species will occur with the development of benthic organisms on the wreck.

The rapid increase of the fish density on new artificial reefs is a common characteristic (Pickering and Whitmarsh, 1997). Bohnsack et al. (1994) reported rapid increases of fish density on new artificial reefs with peak levels occurring within two months. This increase phase lasted eight months in the study of Carr and Hixon (1997). During the present study, a leveling off, characterized by higher fluctuations in numbers, appeared within three months. After the first colonization phase, mean densities (eight to nine fish/m^2) were similar to those reported by Carr and Hixon (1997). This latter result could suggest that the carrying capacity of the CT2 should be around these values with the exception of occasional peaks related to recruitment phases or the sporadic presence of pelagic schools. Bohnsack et al. (1994) also reported rapid increase in biomass. A similar pattern was observed on the CT2. If the mean density of fish on the CT2 remains approximately eight to nine fish/m^2, biomass should increase to more than 300 to 350 g/m^2 with the growth of the surviving recruits and adults.

The initial increase of species richness and density observed on the *Caissons* was probably linked to the effects of the blast of the CT2 on the fish assemblage (migration) and recruitment. However, the observations gathered after the blast showed that it affected a significant number of fish from a limited number of species. These observations were confirmed by the fact that the fish community structure of the *Caissons* was not significantly modified during the survey. After this colonization phase, variations were due to natural processes (recruitment, predation, mortality) and migration of adults to the CT2.

This study showed that species richness is higher on natural reefs than on nearby artificial reefs because of a higher habitat complexity (among others, Chou et al., 1992; Bhonsack et al., 1994; Carr and Hixon, 1997; Chou, 1997; Pickering and Whitmarsh, 1997; Rooker et al., 1997). At the end of the survey, species richness was higher on the CT2, sunk 13 months before, than on the *Caissons*, sunk more than 50 years ago. This result confirms that species diversity is linked to the size and the structural complexity of the artificial reef (Pickering and Witmarsh, 1997), which are more significant on the CT2. The height of the structure acts as a visual or audio stimulant or spatial reference to attract transient species (Pickering and Withmarsh, 1997). The structural complexity also influences community diversity by providing numerous shelters with different habitat characteristics (light, crevice, current, etc.).

Densities are higher on artificial reefs than on natural reefs (Chou et al., 1992; Bohnsack et al., 1994; Pickering and Whitmarsh, 1997). However, Carr and Hixon (1997) found contrasting results because they studied small artificial structures (4 m^2) with limited habitat complexity. Bohnsack et al. (1994) compared similar artificial reefs of different sizes. They found higher density on the smallest structures. In the present study, the density was higher on the CT2 (largest structure) than on the *Caissons* (smallest structure) because the two structures were not of the same type.

Biomass is higher on artificial reefs than on natural reefs, reflecting the attraction of benthic and pelagic predators (Chou et al., 1992; Pickering and Whitmarsh, 1997; Rooker et al., 1997). The highest biomass on the largest structure was also reported by Bohnsack et al. (1994).

Species Similarity and Fish Assemblages

The fish community of the natural reef (*Ricaudy*) had few species in common with the two artificial reefs studied (CT2 and *Caissons*). The species assemblage structures were also different. The species characterizing the *Ricaudy* fish community are usually found on flourishing shallow fringing reefs (Randall et al., 1990; Thollot et al., 1990; Lieske and Myers, 1995; FishBase, 1997). This confirms the observation that the greater the difference in geomorphologic characteristics of habitats, the greater the difference between natural and artificial reef fish assemblages (Chou et al., 1992). In the present study, the artificial reefs are deeper than *Ricaudy*, which has an influence on the resident species that colonize on the artificial reefs (Rooker et al., 1997).

Organic matter and phytoplankton productivity are linked to artificial reef productivity (Bombace et al., 1994). The site where the CT2 was sunk is a productive environment under terrigenous influence. This productivity explains the presence of numerous planktivores (Clupeidae, Caesionidae, Pomacentridae) and their predators (Carangidae) on the wreck and on the nearby *Caissons*. Current patterns also play an important role in the attraction of fish species. Small pelagic species are attracted by current variations and vortex around artificial reefs (Vik, 1982; Bleckman, 1986). The CT2 lies perpendicular to the main currents, which are directed from the hull to the deck. This optimizes the attraction effects of the currents. Juvenile and small fish colonize the deck and the upperworks where the current is weaker.

Fish assemblage on artificial reefs is related to the habitat where they are located (Chou et al., 1992; Pickering and Whitmarsh, 1997). Because the CT2 and the *Caissons* are located in the same habitat and in close proximity, they have similar species assemblages. As the assemblages are also linked to the artificial reef type (Chou et al., 1992; Pickering and Whitmarsh, 1997) and its age, differences were observed between CT2 and *Caissons* assemblages. The fish assemblage of the *Caissons* is the result of 50 years of colonization despite the effects of the blast of the CT2. More sciophilous species (Apogonidae) were seen on the wreck where there are numerous dark shelter areas. More "secondary" species (*Cephalopholis* spp) were observed on the *Caissons* from the beginning of the survey where a diversified benthic flora and fauna have colonized the hard substrate over 50 years.

Ecological Changes

Three categories of species colonized the CT2. The first category regroups pelagic (Carangidae, Scombridae) and opportunist (Lutjanidae, Lethrinidae) species. The former finds food on the wreck and the latter, shelter. The second category concerns small resident reef species (Apogonidae, Chaetodontidae, Pomacentridae, Labridae, Scaridae, among others). The third category consists of large reef species (Serranidae, Acanthuridae and Siganidae) which can venture away from the reef. The relative importance of these species in the assemblages varied over time.

The pioneer assemblage was characterized by the recruitment of juveniles (Clupeidae, Apogonidae, Pomacentridae) on a vacant biotope and the attraction of large adult fish (Carangidae, Lutjanidae, Lethrinidae) from the *Caissons* and the surrounding lagoon. This pioneer assemblage underwent some modifications with the attraction of other pelagic and opportunist species (Carangidae, Sphyraenidae, Scombridae) and the arrival of new recruits (Apogonidae, Pomacentridae). This colonization phase was characterized by variations in the relative abundance of these species related to recruitment and predation intensity. Apogonidae, for example, were always abundant but changes in dominant species occurred.

The secondary assemblages corresponded in diversification with the colonization of secondary and late species (Chaetodontidae, Pomacentridae, Scaridae, Siganidae, Ostraciidae, Tetraodontidae). The development of benthic flora and fauna modified the habitat characteristics, contributing to an increase in complexity of the ecosystem. This probably created new ecological niches suitable for these fish species. Since then fish assemblage has been the result of several processes. There was an interspecific competition to inhabit different parts of the wreck: Apogonidae invaded the dark parts; *Neopomacentrus* spp and *Chromis fumea* constituted small monospecific schools on the deck and around the upperworks where the current is weaker; and Clupeidae and Caesionidae formed large schools above the wreck. The relative importance of the recruiting species and their predators fluctuated as a result of recruitment inputs and predation processes that were observed during the sampling. In the last sample, a recruitment of *Chromis fumea* occurred, which was similar to the one observed during the first sample. These processes will probably continue each year with their importance depending on the interannual recruitment variations.

The ecological changes should not lead to the disappearance of pioneer species in the case of the CT2. These species are still present on the *Caissons* sunk more than 50 years ago. This ecosystem evolved with the colonization of secondary and late species not present on the CT2 (Serranidae), which are more specialized and require more precise habitat characteristics. However, pioneer species remained because of the seasonal recruitment processes and the attraction of their predators. The benthic flora and fauna communities of the CT2 should evolve and become similar to those of the *Caissons*. This trend should lead to the colonization of late fish species, such as those present on the *Caissons*. This is the evolving part of the ecosystem which characterizes the secondary assemblages. Only a few studies examined ecological changes during the colonization of an artificial reef by a fish assemblage. Cumming (1994) reported that succession, as described by Odum (1969), did not proceed beyond the earliest stages on an artificial reef in an environment with frequent physical disturbance. The ecosystem described by Cumming (1994) remained at a secondary stage and late

assemblages did not replace secondary ones, which is quite similar to what was observed during the present study.

Management Implications

This survey brings new data on the attraction-production debate. Attraction of large adult fish from surrounding habitats is confirmed. The CT2 was sunk on bare sand with a nearby oasis (*Caissons*) acting as an aggregating device for recruits of adult fish. However, the productivity of the artificial reefs is still questionable. The artificial reef should be productive if habitat is a limiting factor in the surrounding environment. In this case, the artificial reef will provide space for recruits that would not have otherwise recruited. The species concerned are mostly demersal, territorial reef species. In the present study, CT2 and *Caissons* artificial reefs are located in a productive coastal zone and acted as a recruitment area for small pelagic and demersal reef species. For the former (Clupeidae, Sphyraenidae), the presence of the artificial reefs did not increase productivity of the surrounding lagoon. These juveniles probably would have recruited in the coastal zone even if the artificial reefs were not present. For the demersal reef species (Apogonidae, Pomacentridae), the artificial reefs were more likely to increase production because the pool of recruits appeared to be much more important than the available space for settlement in the area. The recruitment of these juveniles increased the productivity of the environment by high predation on the recruits and the surviving adults. In the present study, these demersal species were not abundant so the productivity increase induced by the wreck should mainly be a result of predation processes.

Local authorities now consider the scuttling of the CT2 to be a success. The fish assemblage has increased rapidly and daily dives are organized by dive centers on the CT2 - *Caissons* assemblages inducing economical benefits. However, we recommend planning a baseline survey in the future, before artificial reefs are sunk, to choose the best suitable site. We also recommend avoiding the use of explosives that may cause substantial mortality if a diversified fish community is present in the area.

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ATOLL RESEARCH BULLETIN

NO. 486

FIRST RECORD OF *ANGUILLA* GLASS EELS FROM AN ATOLL OF FRENCH POLYNESIA: RANGIROA, TUAMOTU ARCHIPELAGO

BY

RAYMONDE LECOMTE-FINIGER , ALAIN LO-YAT AND LAURENT YAN

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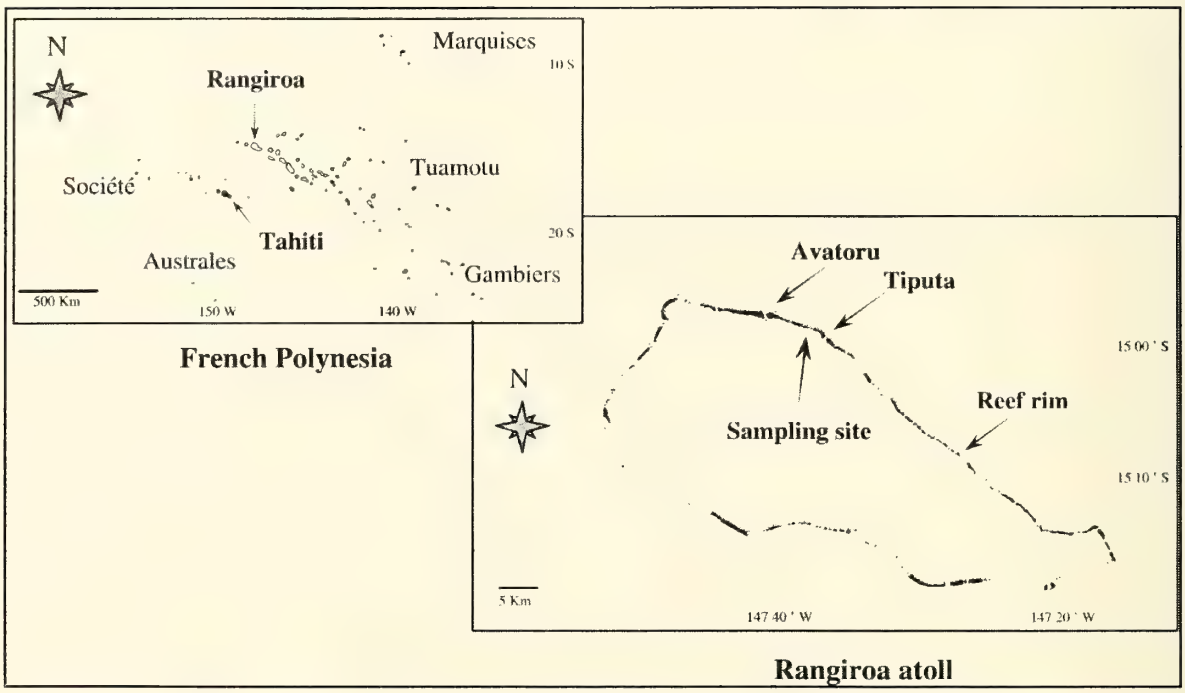

Figure 1. French Polynesia with Rangiroa Atoll, Tuamotu archipelago.

FIRST RECORD OF *ANGUILLA* GLASS EELS FROM AN ATOLL OF FRENCH POLYNESIA: RANGIROA, TUAMOTU ARCHIPELAGO

BY

RAYMONDE LECOMTE-FINIGER[1,2], ALAIN LO-YAT[3] and LAURENT YAN[3]

ABSTRACT

Few observations of glass eels in French Polynesia have been recorded. While conducting a reef-fish larvae survey off the Rangiroa Atoll rim flat, two glass-eel species were caught for the first time: *Anguilla marmorata* and *Anguilla obscura*.

INTRODUCTION

Several records exist of glass eels caught during their migration to the freshwaters in Pacific islands. Migration of glass eels is well known in islands such as Tahiti (Marquet, 1992) but a lack of information about it still remains in atolls .

Rangiroa Atoll is one of the largest atolls in the world and the most important of Tuamotu Archipelago (Ricard, 1985). It is 70 km long and 30 km wide. The peripheral rim is 225 km long and one-third of the rim is above the sea surface (500 to 800 m wide). Lagoon waters flow out through two passes (Tiputa and Avatoru: Fig 1) and oceanic waters flow into the lagoon through channels, called hoas, over the atoll rim.

Studies on larval species, larval flux and recruitment processes of coral-reef fishes in French Polynesia have been undertaken for 10 years on Moorea Island. The colonization of fish larvae in lagoons of atolls or islands occurred only at night during moonless periods (Dufour, 1992). A comparison of the colonization has been made on Rangiroa Atoll since 1989 (Lo-Yat, per. com.) according to Dufour's method (1992). This is the first record and study of glass eels from an atoll.

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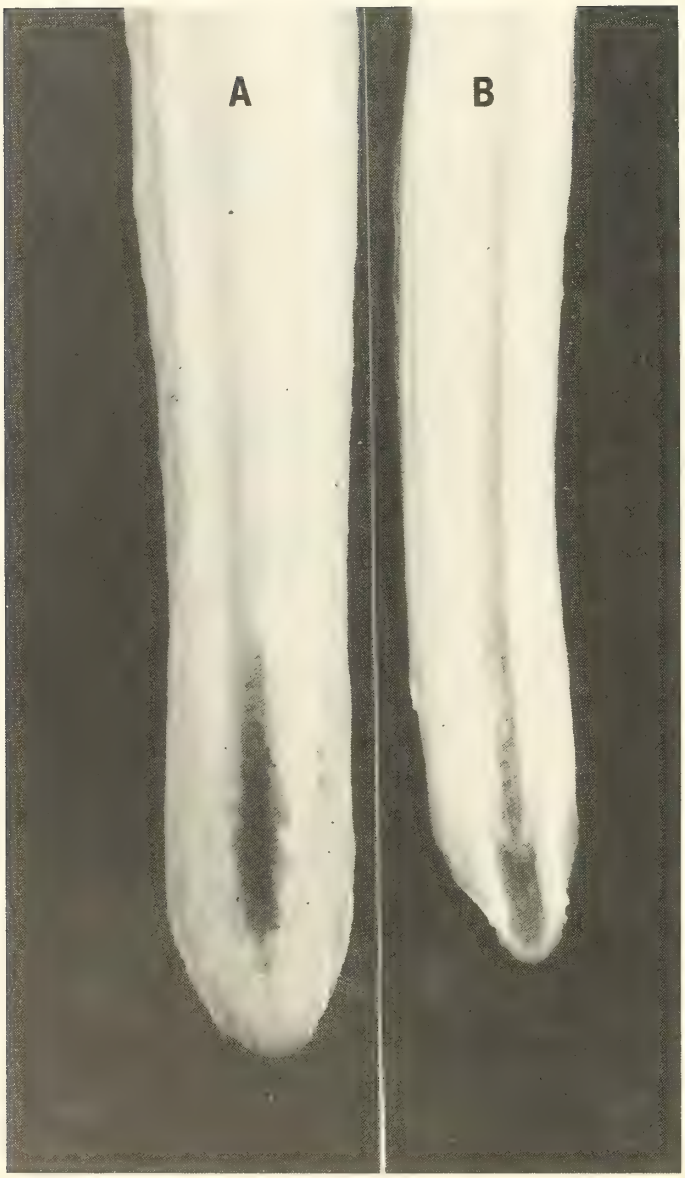

Figure 2. Medio lateral pigmentation in caudal region of *Anguilla marmorata* -A- and *Anguilla obscura* -B-.

METHODS

Coral reef larvae were collected off the northern coast of Rangiroa Atoll (15°S, 147°W) at night with a crest net (Dufour, 1992) that filtered the water coming from the ocean into the lagoon. It was located in a channel (hoa) over the atoll rim, midway between two passes (Fig. 1). Sampling was made from January to April 1998. Animals were preserved in 95% alcohol. Eel traps were put in the two passes, but no glass eels were caught. Moreover, during the daytime, no glass eels were caught in the traps or in the crest nets.

Eel identification is based on characters defined by Ege (1939), Marquet (1992) and Budimawan (1997). Morphological criteria (total length, distance between origins of dorsal and anal in percent of total length) and caudal pigmentation were used (Elie *et al*, 1982; Marquet, 1992; Budimawan, 1997). Total body length was measured to the nearest mm. Vertebrae were counted using micro-X ray (Sigma 2060).

Table 1. Glass eels morphometric data. TL=total length in mm, AL-DL/TL=ano-dorsal length in percent of total length, *A. obsc=Anguilla obscura*, *A. mar.=Anguilla marmorata*.

Date	TL mm	AL-DL/TL%	Species
24/01/98	45	4.1	*A. obsc.*
03/02/98	50	20.0	*A. mar.*
	50	20.0	*A. mar.*
28/02/98	52	15.3	*A. mar.*
	50	4.0	*A. obsc.*
	50	2.0	*A. obsc.*
	48	4.2	*A. obsc.*
	49	4.08	*A. obsc.*
	53	16.9	*A. mar.*
27/03/98	48	16.7	*A. mar.*
21/04/98	52	17.3	*A. mar.*
	54	15.0	*A. mar.*
	50	15.0	*A. mar.*

RESULTS

A total of 13 glass eels were sampled. All specimens sampled were glass eels at VB stage (according to the pigmentation scale of Elie et al., 1982), the first "continental" stage of the eel. Measurements of the morphological characters (Table 1), the tail pigmentation (Fig. 2), and the vertebrae number (106.2 ± 2.8) indicated that two species were present: *A. marmorata* and *A. obscura*. The total length at arrival varies from 45 mm to 54 mm. Glass eels migrate at night towards the lagoon through the channel.

DISCUSSION

The life cycle of eels is believed to conform to the following patterns. Spawning occurs in the ocean. The first larvae, known as leptocephali, migrate across the ocean towards coastal waters. The leptocephali transform into glass eels and cross the interface between the ocean and the continents to begin their growth period mainly in fresh or brackish waters. At this stage the glass eels become pigmented, complete their metamorphosis and turn into elvers and then yellow eels. Once these eels approach maturity, they turn into the so-called silver stage, cease feeding and migrate back to the spawning grounds. Many studies have been published mostly on the species *Anguilla anguilla, A. rostrata, A. japonica, A. marmorata, A. bicolor.* Their spawning areas are now more or less well-known (Schmidt, 1922; Jespersen, 1942; Tsukamoto, 1992; Budimawan, 1997). In contrast, breeding areas for the other species are still hypothetical.

The biodiversity of the *Anguilla* genus is maximal in the Pacific with 16 species present out of a total of 19 (Ege, 1939). French Polynesia covers a vast oceanic area located at the eastern limit of the Indo-Pacific ocean. Five archipelagoes form French Polynesia, an area of 4,000 km^2 scattered over 2,500,000 km^2 of ocean and made up of 34 high volcanic islands and 84 low coral atolls. According to Marquet and Galzin (1991), three eel species are present in French Polynesia: *Anguilla marmorata* (Quoy and Gaimard, 1824), *A. megastoma* (Kaup, 1856) and *A. obscura* (Gunther, 1871). Previous to this report, the known eels from Rangiroa Atoll consisted of two species described from adults (Marquet and Galzin, 1991). *A. marmorata* and *A. obscura* found only in stagnant waters, the Vaimate laguna and on the site of the disused fish-breeding station of Pavete near Avatoru. *A. marmorata* is one of the most common species of Indo-Pacific tropical eels. It is widespread in the Indo-Pacific archipelagoes (Ege, 1939; Jespersen, 1942; Tesch, 1977; Delsman, 1929; Takahasi, 1915; Chevey, 1936; Jubb, 1964; Kiener, 1981; Marquet and Galzin, 1991; Marquet *et al*, 1997). *A. obscura* inhabits only the Pacific ocean (Ege, 1939). Adult specimens of these two species were caught in different sites in French Polynesia. Both species are found respectively in Austral, Gambier, Society and Tuamotu Archipelagoes, and only *A. marmorata* in Marquesas Archipelago (Marquet and Galzin, 1991).

Several records exist of tropical glass eels (*A. marmorata, A. megastoma, A. obscura*) during their anadromous migration to the island of Tahiti (Marquet, 1992). There are no similar reports for migration to atolls. This is the first record of glass eels

not only from an atoll of French Polynesia but from any atolls in the Pacific. Despite the low number of glass eels, this record provides important ecological information on the process of inshore migration of tropical eels. Glass eels enter the lagoon over the reef rim by the channel (or hoa) like the other coral fishes (Dufour, 1992) at night. The short length of the new glass eels indicates the existence of a spawning area not far from the atoll. The spawning sites could be situated east of the Tuamotu Archipelago according to Jespersen (1942), Marquet (1992), and Budimawan (1997). Our first record of glass eels in this region seems to corroborate this hypothesis. However, the lack of data on glass-eel migrations and the small number of specimens preclude definite conclusions.

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ATOLL RESEARCH BULLETIN

NO. 487

BENTHIC ECOLOGY AND BIOTA OF TARAWA ATOLL LAGOON: INFLUENCE OF EQUATORIAL UPWELLING, CIRCULATION, AND HUMAN HARVEST

BY

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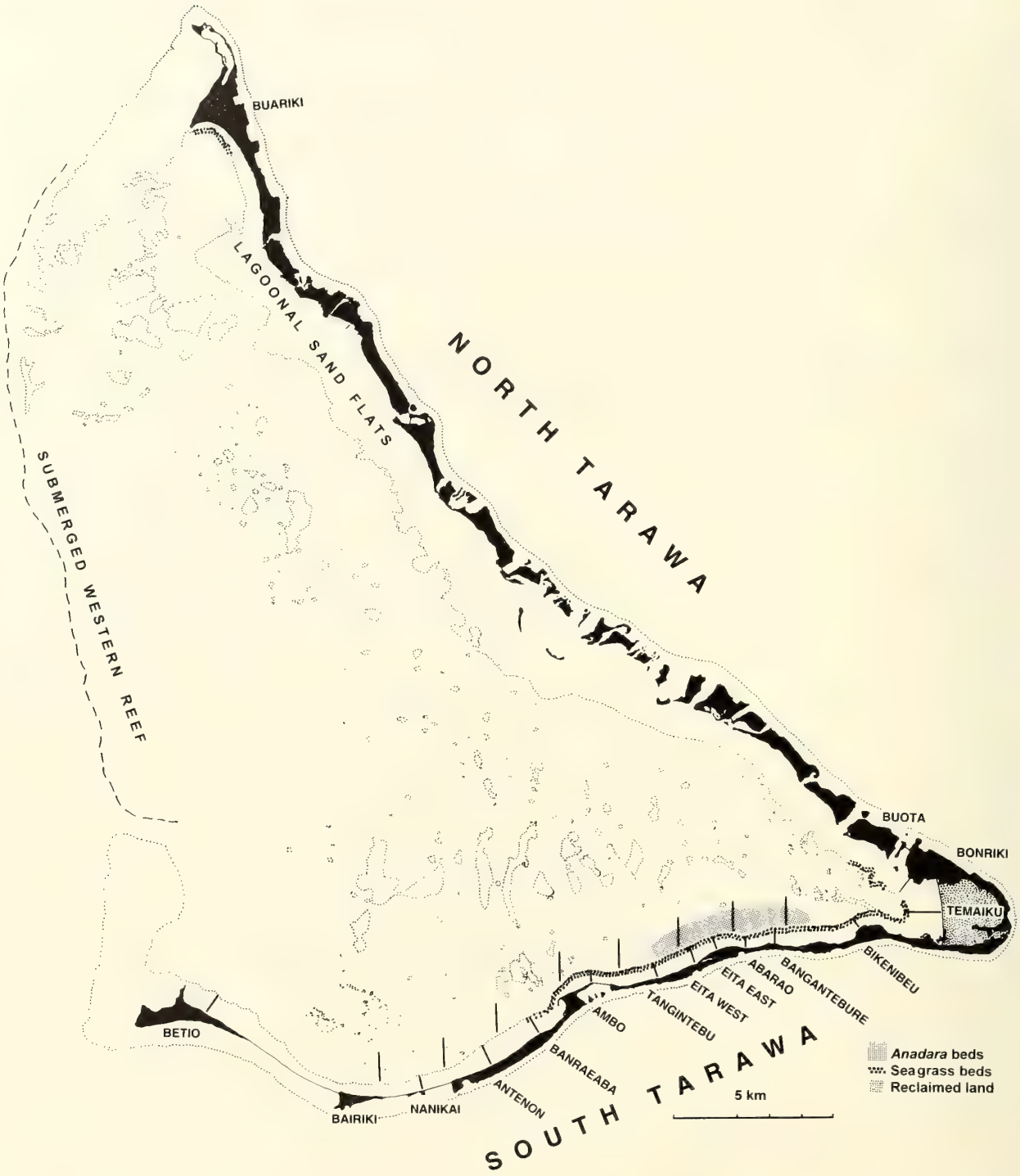

Figure 1. Map of Tarawa Atoll, with main habitat types, offshore Anadara bed, and locations of sand-flat and lagoon-slope transects (short lines) indicated. The 12 sand-flat transects are referred to by the adjacent islet name; lagoon-slope transects are numbered 1-9 west to east (see Appendix I for coordinates of all). Thin lines connecting islets represent causeways. Not all patch reefs and shoals have been charted. True North toward top of page.

BENTHIC ECOLOGY AND BIOTA OF TARAWA ATOLL LAGOON: INFLUENCE OF EQUATORIAL UPWELLING, CIRCULATION, AND HUMAN HARVEST

BY

GUSTAV PAULAY[1,2]

ABSTRACT

The lagoon of Tarawa harbors the richest benthos documented for any Pacific atoll. The biota is strongly influenced by its setting in the equatorial upwelling zone and the unusual geomorphology of the atoll, with a submerged western rim, but largely closed and islet-strewn eastern and southern sides. As the metropolitan center of the Republic of Kiribati, Tarawa also has the largest human population of any Pacific atoll. These three attributes impose a strong influence on all aspects of the lagoon. The high regional productivity supports unusually high population densities of heterotrophic mollusks and irregular echinoids for an "open" atoll. The dense human population on the atoll relies largely on marine resources for its protein needs. The lagoonal sand flat harbors dense and diverse mollusk communities, particularly in seagrass beds. These communities support an intensive subsistence fishery with an annual harvest of ca. 1,000 tons in South Tarawa. Much of the available biomass of the two preferred species, the blood cockle *Anadara uropigimelana* (*te bun*) and the small conch *Strombus luhuanus* (*te nouo*), is taken. Both the seagrass and shellfish beds appear to have expanded considerably in the past 50 years, likely as a result of nutrient enrichment from the rapidly growing human population. Dense mollusk communities along the southeastern lagoon slope at 2-8 m depth support an intensive commercial fishery that harvests approximately 1,000 tons of *Anadara* per year, again representing much of the available production. Three species of irregular echinoids are conspicuously abundant on the floor of the eastern lagoon, with combined densities >100 m^{-2} in the muddy facies of the inner lagoon. All aspects of the benthos follow a marked west-to-east and north-to-south zonation, reflecting the one-sided exchange of oceanic waters along the western atoll rim. While mollusk and echinoid biomass increases southeastward, coral diversity and cover decreases in that direction.

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INTRODUCTION

Among the many islands that dot the central Pacific, atolls are the most prevalent because the subsidence of the Pacific plate leads to the geologically rapid submergence of high islands, usually with their conversion into atolls. Although roughly similar in origin and structure, atolls nevertheless vary considerably in geomorphology, habitats, and biota. Atoll lagoons show the greatest variation and often differ substantially even from neighboring atolls, while outer reef habitats and biotas tend to be much more similar (e.g., Salvat, 1967; Chevalier, 1976, 1979). Much of this variation is the result of diversity in atoll geomorphology, and attendant diversity of oceanographic and ecological conditions. The nature of the atoll rim (depth, portion covered by islets, number and location of deep passages traversing it) is perhaps the most important variable as it determines the nature of water exchange between the lagoon and surrounding ocean. The degree of water exchange in turn affects many environmental parameters such as water quality, nutrient cycling, productivity, the nature of bottom sediments, sediment production rates, rates of reef growth and erosion, etc. In addition to differences arising from atoll geomorphology, atoll biotas are affected by a variety of other factors. Variation in productivity, both in the surrounding ocean and lagoon waters, can lead to substantial differences among reefs (e.g. Highsmith, 1980). The impact of humans, rapidly accelerated by growing populations, improved technologies, and the resulting increased utilization of limited resources, also exerts strong influences on reef communities in many areas of the tropics (Wilkinson, 2000).

The purpose of this paper is to describe aspects of the benthic ecology and biota of Tarawa Atoll (Tungaru [former Gilbert] Islands, Republic of Kiribati) and to consider how the unusual setting of the atoll has affected the benthos. This study was part of multi-disciplinary efforts to develop a management plan for the Tarawa lagoon. The benthic surveys carried out were aimed at evaluating the benthic invertebrate resources of the lagoon, their production, and harvest levels. Thus the focus of this paper is on habitats that have important benthic resources and on species that are fished.

Three aspects of Tarawa's environment appear to have especially noticeable consequences on the benthos: 1) The atoll lies in the nutrient-rich waters of the equatorial upwelling area, in an area of high planktonic productivity and biomass (Kimmerer and Walsh, 1981; Kimmerer, 1995). This enrichment has widespread consequences on the atoll, enhancing benthic productivity and biomass, and even affecting the geomorphology of the atoll (see below; Paulay, 1997). 2) Water exchange between the lagoon and surrounding ocean is extensive but largely confined to the submerged west side of the atoll (Fig. 1) (Chen et al., 1995). The directionality of this limited exchange has created marked west-to-east and north-to-south gradients in nutrients, phytoplankton, sediment composition, coral diversity and abundance, bioerosion, etc. across the atoll lagoon (Kimmerer and Walsh, 1981; Kimmerer, 1995; Paulay and Kerr, 2001). 3) As the metropolitan center of Kiribati, Tarawa has one of the densest populations among Pacific atolls. This has lead to varied impacts including heavy fishing pressure on marine organisms, sewage-derived microbial pollution, and localized nutrient enrichments along the nearshore sand flat (Kelly, 1993).

Previous work on the benthic marine biota of Tarawa and neighboring atolls is limited. Zann and Bolton (1985) described the ecology of *Heliopora* and quantitatively described the reefs around Betio on Tarawa. Zann (1982) described the marine ecology of the Betio area and provided a checklist of reef corals there prior to the construction of the large Betio-Bairiki causeway. Bolton (1982a) described the epifauna and infauna of the intertidal lagoonal sand flat fronting the islets of South Tarawa. Numerous other shorter technical reports describe aspects of economically important shellfish (including giant clams and pearl oysters), bêche-de-mer, and fishes on Tarawa (see Gillett et al., 1991).

Randall (1955) reviewed the fishes of the Tungaru Archipelago, and Banner and Randall (1952) described the marine biology of Onotoa Atoll, south of Tarawa. Lobel (1978) (as well as Banner and Randall) reviewed the indigenous names of marine organisms in Kiribati. Among the island groups surrounding Tungaru, the marine biota of the Marshall Islands to the north have been extensively studied (e.g., Devaney et al., 1987), while the marine biota of Nauru to the west and Tuvalu to the south are poorly known. Canton Atoll (Phoenix Islands) and Fanning Atoll (Line Islands) (both now part of the Republic of Kiribati) to the east have been the subjects of multidisciplinary studies by teams from the University of Hawaii, summarized in issues of Atoll Research Bulletin (1978 [No. 221]) and Pacific Science (1971 [25:2] and 1974 [28:3]), respectively. These atolls have special relevance to Tarawa because they also lie in waters influenced by equatorial upwelling.

Tarawa is a triangular atoll, with a wide reef rim on the eastern (called North Tarawa locally and hereafter) and southern (called South Tarawa locally and hereafter) sides bearing a near-continuous chain of islets, and a largely submerged barrier reef forming the west side (Fig. 1). The submerged barrier reef lies at a depth of several meters, shallowing northward, and is traversed by a deep channel near its southern end. The benthic habitats of Tarawa Lagoon can be divided into four major categories: 1) the intertidal to shallow subtidal sand flat that fronts the lagoonal sides of islets and passages along the southern and eastern sides of the atoll; 2) the lagoon slope and floor that cover much of the lagoon interior; 3) the patch reefs and shoals that rise from the lagoon bottom; and 4) the submerged barrier reef that forms the western atoll rim (Fig. 1). An extensive, largely intertidal, outer reef flat is also developed along the ocean side of the islets lining the southern and eastern rim. These outer reef habitats were not surveyed and are not considered further here. Here I deal mostly with the soft-bottom habitats of Tarawa lagoon; reef habitats, including fringing reefs, patch reefs and shoals, and the western barrier reef, are discussed in Paulay and Kerr (2001). The major habitat types of the lagoon are first reviewed below, followed by an analysis of the impact of human gathering pressures on invertebrate populations.

METHODS

Sand Flat

The sand flat was studied through quantitative surveys, qualitative examination of the fauna, and mapping of seagrass beds from aerial photographs. Because the primary purpose of our surveys was to evaluate the shellfish resources of this habitat in South Tarawa, quantitative surveys focused on mollusks.

Fifteen transects with nine stations each were set perpendicular to shore at regular intervals along the length of South Tarawa (Fig. 1; Appendix I). Nine stations were selected on each transect as follows. Stations 1-3 were on the beach slope. Station 1 was halfway between the upper strand line and the lower end of the slope (where it abruptly meets the plain of the sand flat), Station 3 was at the lower end of the slope, and Station 2 was halfway between Stations 1 and 3. Stations 4-6 were spaced equidistantly along the sand flat between Station 3 and the landward end of the seagrass bed, if present. Stations 7-9 were in the seagrass bed, if present. Station 7 was set 5 m lagoonward from the landward margin of the seagrass bed, Station 8 was in the middle of the bed, and Station 9 was 5 m shoreward from the lagoonward margin of the seagrass bed. At locations lacking seagrass beds, Stations 4-9 were evenly spaced along the sand flat, from one-sixth lagoonward of Station 3 to the edge of the sand flat. The field work for the sand-flat survey was carried out mostly by Andy Teem and Nabuaka Tekinano of the USAID project.

Two 0.25 m^{-2} quadrats were placed haphazardly within 5 m of each other at each station. The sediment at each quadrat was excavated to 20 cm deep or until bedrock was reached and the depth of the excavation noted. Sediment was passed through a 2 mm-mesh screen, and all live mollusks and echinoids collected. This process, carried out in the field, was not entirely effective because the abundant lag (large sediment grains retained by the screen) made noticing and picking all of the numerous smaller (<1 cm) mollusks difficult. Thus the data presented here represent minimum estimates only, and actual population densities of especially the smaller species were likely higher. All specimens were identified to species in the laboratory and their maximum length measured.

At many quadrats, including most of those at Stations 1-3, the technicians recorded no shellfish. These quadrats may represent areas devoid of shellfish (for example because of hard bottom), or samples may have been collected but subsequently lost. Most of the missing data are from samples at Stations 1-3 (where lag was excessive and the fauna is poor) and at three of the 15 transects (located at Teaoraereke, Dainippon causeway, and Temakin-Betio; these three transects are not mapped on Figure 1). These stations and transects are not considered further. Because most of the stations and transects that lack data are in areas (i.e., beach slope and western sand flat) characterized by gravelly sediments or hard substrata, the lack of data probably reflects a lack of shellfish, rather than lost collections. The few (5% of the total, $N = 144$) quadrats with missing data at Stations 4-9 in the other 12 transects are therefore assumed to not contain shellfish; an error in this assumption would increase shellfish abundance slightly.

In addition to surveying the infauna, the cover formed by an abundant zoanthid (probably *Zoanthus* sp.) was measured on seven transects (at Betio, Nanikai, Antenon, Ambo, Eita west, Eita east, and Abarao: Fig. 1) in the same quadrats. Zoanthid cover was measured by the line-intercept quadrat method, i.e. by counting what proportion of the 16 string intersection points, set in 0.25-m^2 stringed quadrats, had zoanthids lying under them.

The extent of seagrass beds was evaluated from site visits throughout North and South Tarawa and from aerial photographs (from 1943: housed at the Bishop Museum; from

1984: housed at the Survey Department, Tarawa) for South Tarawa. Most aerial photographs available for North Tarawa did not include the seagrass zone.

Lagoon Slope

The gently sloping lagoon bottom bordering the lagoon sand flat in South Tarawa supports a dense community of *Anadara* clams that forms the basis of a substantial, canoe-based, diving fishery (see below). The lagoon slope, defined as the area within 1 km of the lagoonward edge of the seagrass beds that form the sand flat margin, was surveyed to evaluate the geographic spread of these beds and to identify the macrobiota associated with them.

Two surveys were run to characterize the benthos of the South Tarawa lagoon slope. The first ran along the length of the southern rim, while the second focused on the major known *Anadara* beds. The first was carried out mostly by Andy Teem and Nabuaka Tekinano of the USAID project, and the second jointly by them and the author. In the first survey, nine transects, oriented north to south, were run on the lagoon slope at evenly spaced locations between Nanikai and Bikenibeu (Fig. 1; Appendix I). On each transect, paired 0.25 m^2 quadrats were haphazardly placed on the bottom at five stations located by Global Positioning System (GPS) at 0.05' (minutes of latitude, which represents 90 m), 0.15', 0.25', 0.35', and 0.55' north of the lagoonward end of the seagrass beds. Depth and GPS location were recorded for each station (see Appendix I). Within each quadrat, divers searched for large (>2 cm) mollusks and echinoids, visually and by hand, to a sediment depth of approximately 10 cm. This method is faster and just as effective as sieving for large mollusks and echinoids. Collected specimens were identified and measured in the laboratory.

The second survey focused on the *Anadara* bed offshore of Tangintebu-Bangantebure (Fig. 1). A series of rapid spot dives were conducted from east to west across this bed to establish its length followed by four north-south passes to establish its width. Finally, the population density of larger mollusks and echinoids was surveyed at 10 haphazardly selected stations within the bed, with four replicate 0.25 m^2 quadrats at each, using the method described above.

Lagoon Floor

The lagoon floor was surveyed at 14 stations set up to lie in three east-west lines across the atoll (Figure 9; Appendix I). At each station, two divers swam for five minutes and recorded or collected the conspicuous macrofauna. Two 0.25 m^2 quadrats were then haphazardly placed for quantitative enumeration of smaller macrofauna, and the larger epibenthic species (mostly irregular echinoids) in each collected. The bottom sediment within each quadrat was then excavated to a depth of ca.10 cm, taken on board in a large bag, and sieved through a 2 mm-mesh screen. This survey was carried out by Alex Kerr, Nabuaka Tekinano, Andy Teem and the author.

Mollusks and echinoids were the dominant fauna retained by the 2 mm-mesh screen, although small polychaetes were visibly abundant on the bottom. Species were identified, and shell and test lengths were measured for all mollusks and echinoids to the nearest mm.

Gatherer Surveys

Shellfish are an important part of the diet on Tarawa and the productive lagoon provides abundant stocks that are easily accessible even to people with no fishing equipment. Landing surveys were conducted to evaluate the type and intensity of gathering pressure on shellfish.

Surveys were implemented to count the number of people collecting shellfish and to measure the weight and species composition of their catches. Both types of surveys were implemented for gatherers on the South Tarawa sand flat and for divers on the offshore Tangintebu-Bangantebure *Anadara* bed. Qualitative observations and brief interviews with gatherers also were conducted whenever possible.

To measure the catch of people collecting on the sand flat, technical personnel of the USAID project intercepted gatherers at 13 locations along the shore of South Tarawa as they arrived from collecting trips to the sand flat. The number of gatherers who contributed to each catch, the time spent gathering, the habitat (nearshore-sand flat, mid-sand flat, seagrass bed, or deep lagoon) where they gathered, and the time of arrival were recorded based on information provided by the gatherers. Each catch was weighed as a whole, and the weight and number of individuals of each species were determined from either the whole catch or a subsample. The maximum shell length of a haphazard subsample of 20 (or the number available, whichever was greater) shells of each species in each catch was measured with calipers to the nearest mm. Because not all samples were processed with equal thoroughness, not all this information is available for every catch. Where the number of individuals of a single species was recorded within a catch, but the total weight of that species within the catch was not determined, the latter figure was estimated from the average weight per shell for the given species, as determined from other samples.

We counted the number of gatherers working the Tangintebu-Bangantebure *Anadara* bed from a boat on six occasions by skirting all vessels seen in the area and counting the number of divers associated with each. The harvest of divers working the Tangintebu-Bangantebure *Anadara* bed was largely determined by interviewing divers on-site. This method was more effective than a landing survey because, with only a few vessels working the area, their catches would have been difficult to intercept on shore. In addition, the standard-sized rice bags (holding 34 ± 1.5kg per bag; $N = 5$) that divers use to hold shellfish allow for a fairly accurate assessment of catch size.

To estimate the number of people gathering on the sand flat, I counted gatherers from the western tip of Betio to the tip of the Bonriki jetty from a series of vantage points that allowed observations throughout the entire sand flat. These counts were made around low tide by driving from one end of South Tarawa to the other, and were probably >90% accurate for that time. Six such counts were made.

Unless otherwise noted, data are given as mean ± 1 standard error (SE). Coordinates of quantitative stations and transects are given in Appendix I. Author and year of species

discussed in text are given in Appendix II, together with a listing of invertebrates for which I was able to get I-Kiribati names.

RESULTS AND DISCUSSION

Sand Flat

Physiography and habitats

The extensive intertidal to shallow subtidal sand flat that borders the lagoon ranges from approximately 300 m to 2.5 km wide and harbors dense communities of infaunal invertebrates (Bolton, 1982a; below). The sand flat fronting the lagoonal sides of islets in South Tarawa differs from that in North Tarawa. The former averages about half the width of the latter (< 1 km vs. typically 1-2 km), has a more extensive marginal seagrass bed, and has poorer fringing-reef development off its lagoonal margin. The two areas must also have differences in the benthos; however, as our surveys were limited largely to South Tarawa, these remain to be documented.

The sand flat is dominated by poorly sorted coarse sands with abundant gravel comprised of shells and coral fragments (Weber and Woodhead, 1972; Richmond, 1990). The sand flat in South Tarawa can be demarcated into three zones: 1) a relatively steep beach slope; 2) a wide, gently sloping plain constituting the bulk of the sand flat; and 3) seagrass beds developed along the lagoonal margin of the sand flat in many, but not all, areas. Some nearshore areas of the sand flat (especially in the southeastern "elbow" of the atoll and along sections of North Tarawa) support stands of shrub-sized mangroves (*Rhizophora mucronata*) with dense fiddler-crab populations.

The gentle slope of the sand flat abruptly gives way to the steeper lagoonal slope at approximately 0.5-1 m below lowest low water, at the lagoonward edge of the seagrass bed, if present. Although no living corals were seen on the sand flat, the adjacent lagoonal slope supports scattered colonies or clumps of colonies of corals, mostly *Porites* spp. and *Pocillopora damicornis*, in South Tarawa. In North Tarawa this zone often has contiguous fringing and patch reefs that are generally more diverse and tend to be dominated by *Acropora*.

Seagrass Beds

Extensive beds of the seagrass *Thalassia hemprichii* are developed along the lagoonal margin of the sand flat in southeastern Tarawa Lagoon and are the focus of much of the shellfish harvesting effort there (see below). The abundance of bivalves in the seagrass beds is striking, and many of the best shellfish grounds are clearly in areas of seagrass abundance. Seagrasses are well known to host a greater abundance of benthos than surrounding soft bottoms because: they serve as refuges from predation; provide greater habitat complexity, increased food supplies, and more stable substrata; and create hydrodynamic conditions that are especially favorable for larval settlement (Peterson, 1986; Orth, 1992). Bivalve populations have been found to have greater growth rates within seagrass beds, probably because of increased food supplies (Peterson et al., 1984). Tebano (1990) showed that the density of *Anadara* clams in Kiribati is significantly correlated with

seagrass density; several other shellfish species also appear to show a preference for seagrass habitats.

Seagrass beds extend in a largely unbroken band along the eastern half of South Tarawa (Banraeaba to Bikenibeu), are somewhat discontinuous along the atoll's southeastern "elbow" (Bikenibeu to Buota), and are widespread again at the north end of the lagoon (around Buariki) (Fig.1). These areas correspond to the locations of the longest islets on Tarawa. Seagrass beds are rare along the western half of South Tarawa (Betio to Antenon) and along most of North Tarawa. The only seagrass encountered along the central section of the latter was a single small (a few square meters) patch off Abatao Islet. Aerial photographs from 1943 indicate additional small patches of seagrass lagoonward of the passage between Tabangaroi and Tabonimata islets, but whether these patches survive today is unknown.

Aerial photographs from 1984 show that the average widths of South Tarawa seagrass beds were 100-150 m, reaching a maximum of 250 m. The geographic spread of seagrass beds does not appear to have changed much between 1943 and 1984 in South Tarawa; however, the width of these beds has more than doubled. In 1943, a narrow seagrass bed extended virtually continuously from Banraeaba to Bikenibeu as it does today; however, most of it was <100 m wide. The width of these beds was measured by evenly spaced transects for two stretches that were clearly discernible in photographs from both 1943 and 1984. In the Abarao-Eita stretch, the seagrass bed had increased significantly, from 46 ± 37 m (s.d.) wide in 1943 to 100 ± 52 m (s.d.) wide in 1984 ($N = 2 \times 11$, $P < 0.05$, t test). In the Eita-Taborio stretch, the seagrass bed increased from 43 ± 16 m (s.d.) to 136 ± 47 m (s.d.) wide in 1984 ($N = 2 \times 11$, $P < 0.0001$, t test).

Biota - Mollusks

The South Tarawa sand flat hosts a dense and diverse assemblage of mollusks. Twenty-six mollusk and five echinoderm species were noted in the quantitative surveys, and numerous additional species were noted outside these surveys. Bivalves dominated the fauna both in species richness (20 bivalves versus 6 gastropods) and numerically (93% of mollusk individuals encountered).

The mean population density of 10 species exceeded 1 m^{-2}, averaged over the sand flat (12 transects, Stations 4-9) (Fig. 2). The most abundant species encountered were three small (<2 cm) clams: *Codakia bella*, *Wallucina haddoni*, and *Timoclea marica.* Of these, *C. bella* and *T. marica* are harvested in small quantities. The three most important species for local consumption, *Gafrarium pectinatum* (*te koumara*), *Anadara uropigimelana* (*te bun*), and *Strombus luhuanus* (*te nouo*), were also among the 10 most abundant species.

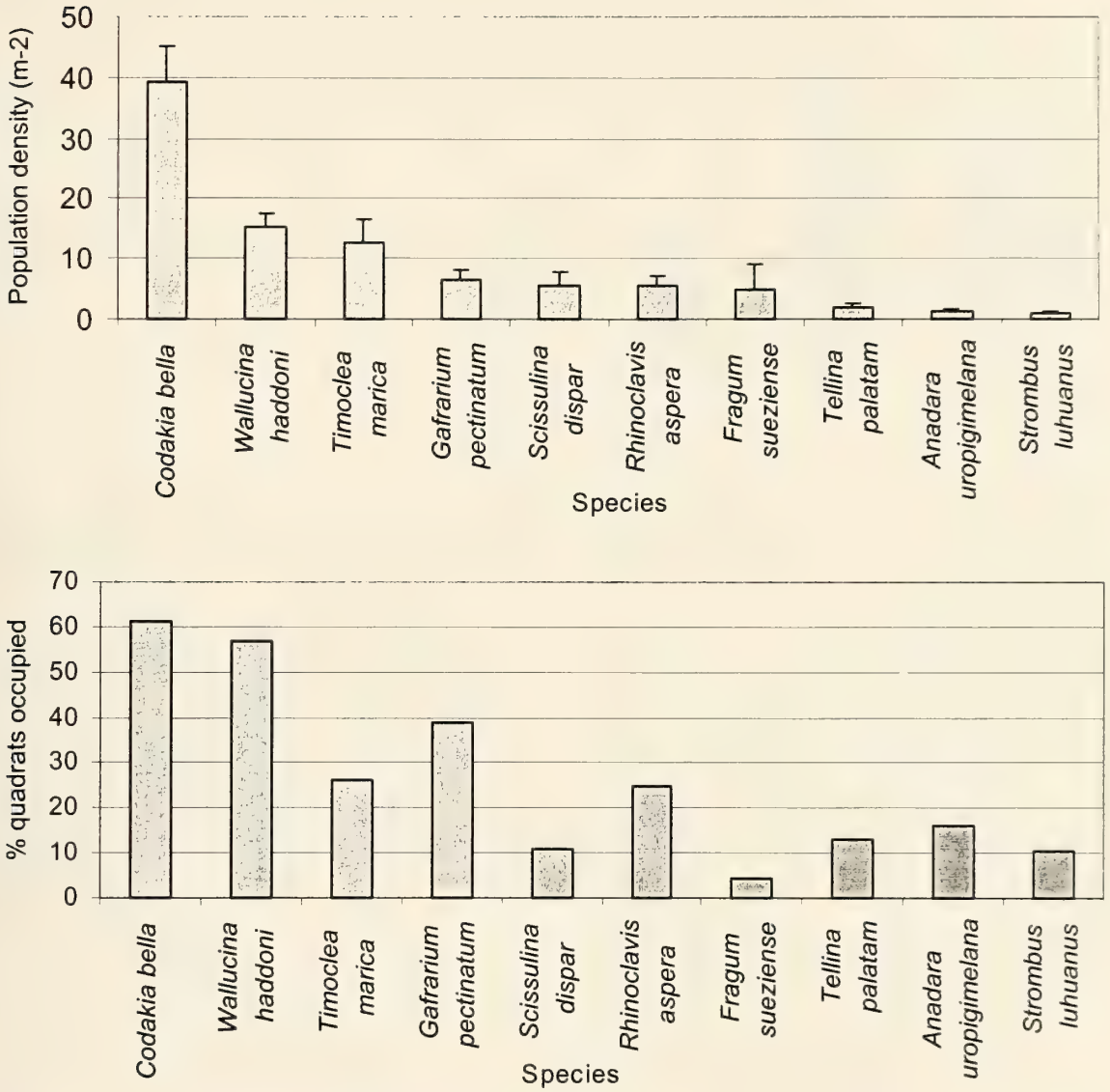

Figure 2. (Top) Mean (± SE) population density of the 10 most common mollusks on South Tarawa sand flat averaged over 12 transects and Stations 4-9 (N = 144 quadrats). Note that the abundance of smaller species here indicated is underestimated (see Methods). (Bottom) Percentage of quadrats in which the numerically most common species were found.

The densities of several species (e.g. the clams *Codakia bella, Gafrarium pectinatum,* and *Anadara uropigimelana*) increased lagoonward across the sand flat and were highest in the marginal seagrass beds. Other species (e.g. the clams *Wallucina haddoni* and *Timoclea marica*) showed less clear trends or were most common at mid-sand flat (Fig. 3). In contrast, a few species, most notably the clams *Atactodea striata* and *Asaphis violascens*, were restricted to the higher reaches of the sand flat and to the beach slope (pers. obs.). The overall abundance of mollusks showed some variation across the sand flat with a moderate increase lagoonward (Fig. 4).

The increased abundance of many mollusks lagoonward could be natural, or it could be the result of greater human harvesting pressures in the higher intertidal zone, which is exposed more frequently to gatherers, than in the lower zone. For abundant and little harvested species such as *C. bella* (Fig. 3), the former explanation is more likely, particularly because lucinid bivalves are known often to prefer seagrass habitats (Jackson 1970). In contrast, for economically important shellfish such as *Anadara*, human harvest is highly likely to contribute at least to zonation. Rough calculations (see below) indicate that a large portion of the standing crop of this and a few other species are taken by humans, supporting the above hypothesis.

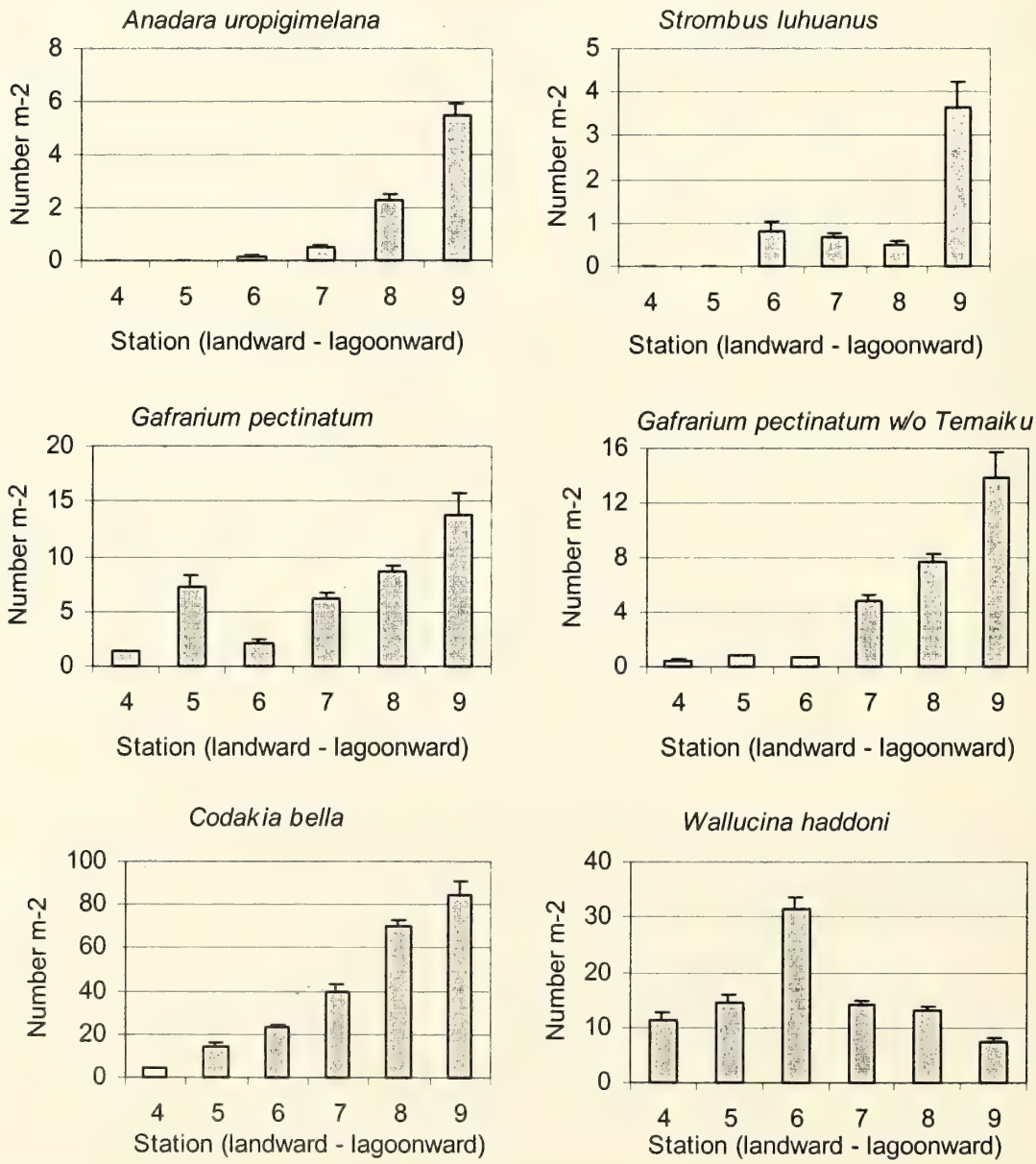

Figure 3. Mean (± SE) population density of selected species across the South Tarawa sand flat from nearshore to lagoon slope margin (Stations 4-9) averaged over 12 transects. *Gafrarium pectinatum* data is shown both in its entirety and without the data from the Temaiku transect (see text for discussion).

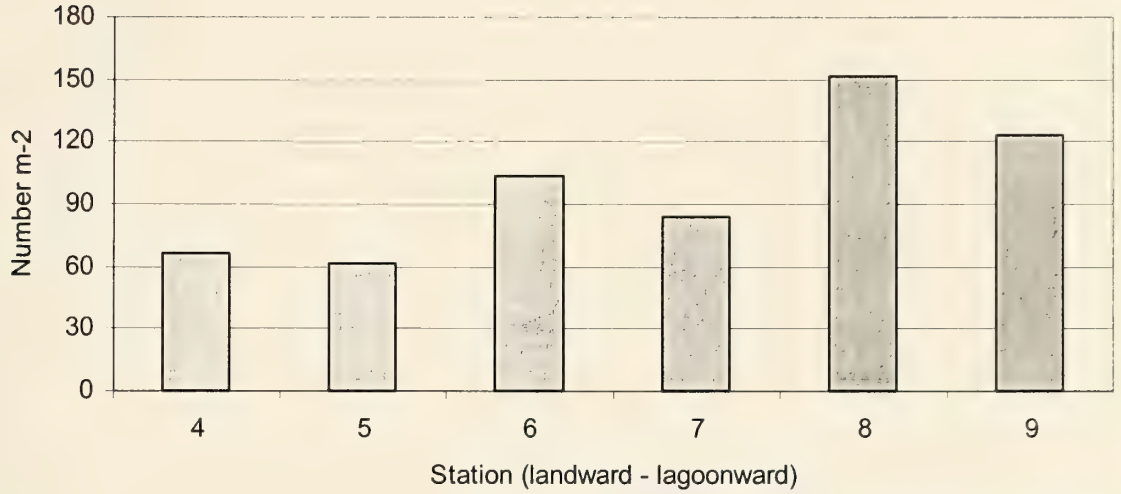

Figure 4. Mean population density of mollusks encountered across South Tarawa sand flat from nearshore to lagoon slope margin (Stations 4-9) averaged over 12 transects.

Economically Important Shellfish Species

Anadara uropigimelana (*te bun*). The shallow-burrowing, endobyssate arcid bivalve, *Anadara uropigimelana* (erroneously identified as *Anadara maculosa* in several past reports from Tarawa), is the most important shellfish resource in South Tarawa (see below; also Tebano and Paulay, 2001). The distribution of *Anadara* (Fig. 5) closely parallels that of seagrass beds (Fig. 1; see below) along South Tarawa. Both are best developed along the eastern half of the South Tarawa shoreline continuously between Banraeaba and Bikenibeu.

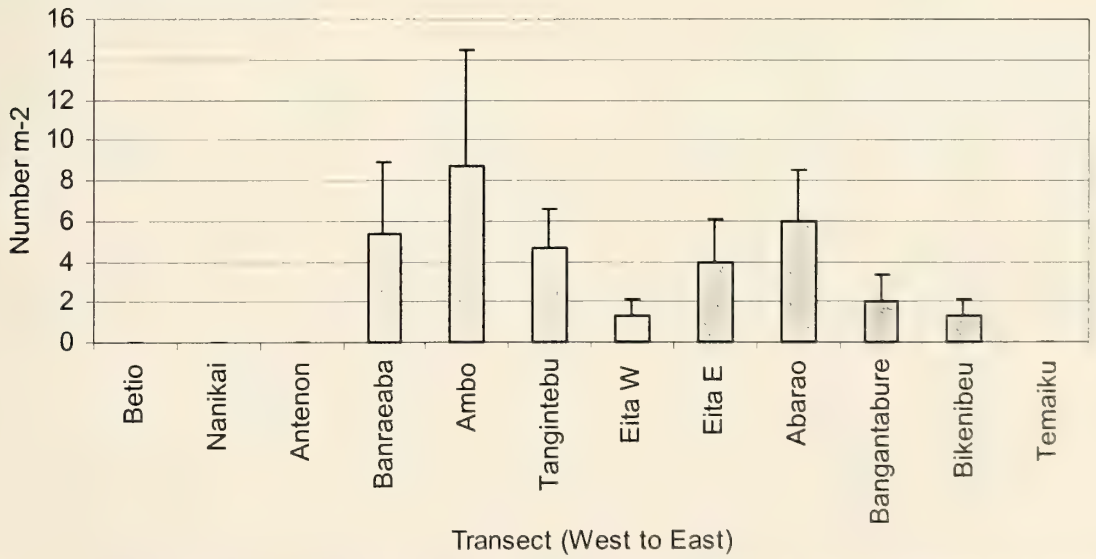

Figure 5. Mean (± SE) population density of *Anadara uropigimelana* among Stations 7-9 along the South Tarawa sand flat, per transect location.

Anadara was found almost exclusively at Stations 7-9, i.e. in the seagrass bed. Its density increased steadily lagoonward within the seagrass bed from 0.75 ± 0.40 m^{-2}

(Station 7; s.d.=1.6)) to 3.5 ± 1.3 m^{-2} (Station 8; s.d.=5.0) and 8.3 ± 2.3 m^{-2} (Station 9; s.d.=9.3). These density values are based only on transects between Banraeaba and Bikenibeu, i.e. in the area corresponding to the main habitat of *Anadara* along the South Tarawa shoreline in the Banraeaba-Bikenibeu seagrass bed. Therefore, these values are larger than those plotted across the entire sand flat in Figure 3. Overall, *Anadara* density averaged 4.2 ± 1.7 m^{-2} (s.d.=6.8) throughout the seagrass bed in this region. Yamaguchi et al. (no date) found comparable densities (means of 0.9-7 m^{-2} at four sites) in 1991. Assuming a seagrass bed approximately 10 km long and 150 m wide, this population density translates to an abundance of approximately 6.3 ± 2.6 x 10^6 shellfish. Because the population extends lagoonward onto the shallow lagoon slope, the total number accessible by wading is considerably larger, however (see Lagoon Slope section below).

Strombus luhuanus (*te nouo*). The epibenthic conch *Strombus luhuanus* was the second most important shellfish in South Tarawa and dominated catches in many areas of the coastline (see below). This conch was restricted largely to the lagoonward half of the sand flat (Stations 6 through 9; see Fig. 3). The distribution of *S. luhuanus* was highly variable among transects and stations surveyed, with an average density of 1.4 ± 0.6 m^{-2} (for Stations 6 through 9; s.d.=5.9). Taken at face value, this density corresponds to an abundance of approximately 7 ± 3 x 10^6 animals along the 20 km long sand flat of South Tarawa, given an approximate habitat width of 250 m. The observed population densities are considerably below those (means of 4.0-30.5 m^{-2} at four sites) encountered by Yamaguchi et al. (no date) in 1991, and also appear low given the tremendous gathering pressure that this species experiences (see below). The high variability in the data, as well as qualitative observations, indicate that the distribution of *S. luhuanus* is patchy on the sand flat, perhaps as a result of the conch's mobility (see below). The presented estimates are based on only 34 specimens encountered in quadrats, and may considerably underestimate the actual abundance of this species.

Gafrarium pectinatum (*te koumara*). Although numerically more abundant than the other two species, the venerid clam *Gafrarium pectinatum* is harvested less frequently, probably because of its burrowing habit and smaller size. Nevertheless, *G. pectinatum* is an important local bycatch and can dominate catches in some areas. The distribution of *G. pectinatum* varied greatly among transects with the Temaiku and Banraeaba transects traversing particularly dense beds (Fig. 6). The Temaiku *Gafrarium* bed, extending across the wide sand flat of the "elbow" of the atoll, is well known and the focus of much gathering activity. *Gafrarium pectinatum* was found at all stations lagoonward of the beach slope and its overall abundance increased offshore (Fig. 3). This species was strikingly more abundant in the seagrass zone than further inshore, except at the unusual Temaiku sand flat (Fig. 3). The mean abundance of *G. pectinatum* across the sand flat (Stations 4-9) was 6.6 ± 1.6 m^{-2} (s.d. = 18.9). Yamaguchi et al. (no date) found comparable densities (means of 0-19.1 m^{-2} at four sites) in 1991. Given the 20 km long and approximately 500 m wide South Tarawa sand flat, the projected abundance of this species is approximately 6.6 ± 1.6 x 10^7 animals.

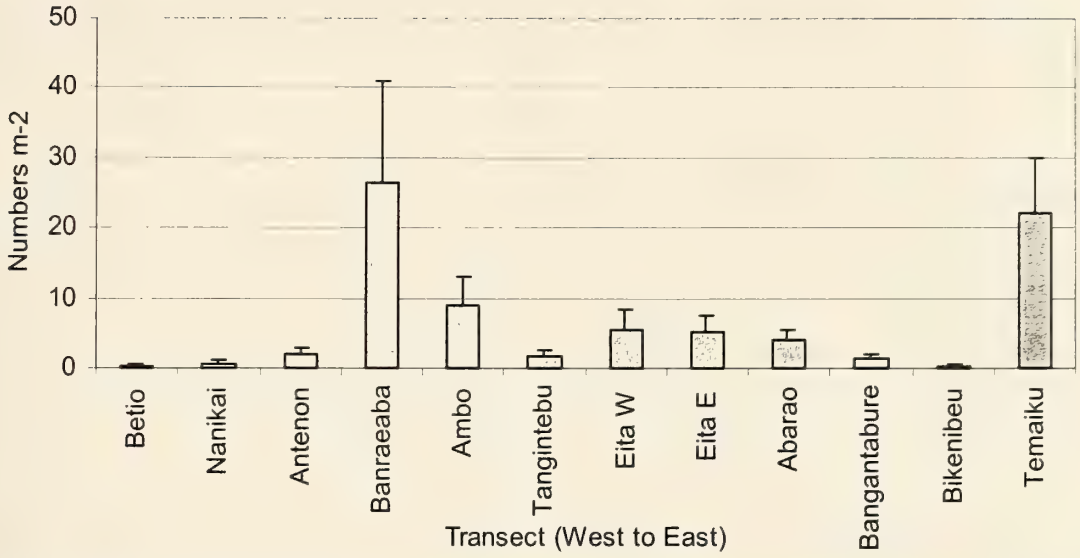

Figure 6. Mean population density (among Stations 4-9) of *Gafrarium pectinatum* along South Tarawa sand flat, per transect location.

Asaphis violascens (te koikoi). This species is restricted to the mid-high intertidal beach slope, an area that was not effectively sampled by our surveys. On Tarawa, *Asaphis* is common in a narrow zone on beaches on the lagoon side and in similar habitats on the ocean sides of islets. It is the dominant, and often the only, bivalve in this habitat. On many islands, *Asaphis* are harvested as single clams, with people searching for the siphonal openings and then extracting the shellfish (pers. obs.). On Tarawa, however, gatherers dig up large areas of suitable habitat, usually with spoons, to uncover all the clams in the area. This difference in method implies that these clams are more abundant on Tarawa (as are many other shellfish) than on many other central Pacific islands, thus making wholesale digging productive. Although we did not observe the abundance of *Asaphis*, the species appears to occur in densities of tens-per-square meter in its habitat, based on observing people digging for it.

Atactodea striata (te katura). This small surf clam is abundant on high intertidal lagoon beaches around Tarawa and is the focus of a minor fishery, mostly as a favored baby food or as a side catch with *Asaphis*. *Atactodea striata* has separate sexes and an extended breeding period in New Caledonia (Baron 1992).

Biota - Other Organisms

In addition to supporting a rich molluscan community, the sand flat harbors a diversity of other invertebrates; however, these species were not studied quantitatively. Bolton (1982a) provides abundance data on a variety of other groups, especially polychaetes and crustaceans; however, many of her identifications appear to be erroneous. A few conspicuous organisms and some species that dominate other habitats on the atoll are discussed here.

Holothurians and irregular echinoids were the only echinoderms encountered on the sand flat during the surveys. Only a single specimen each of three larger irregular echinoids, *Maretia planulata*, *Laganum depressum,* and *Metalia sternalis*, were encountered in the quantitative surveys. These species may be more common locally near the lagoonward end of the sand flat and they dominate deeper lagoon waters (see below). Three holothurian species, *Holothuria atra*, *Bohadschia vitiensis*, and *Holothuria pardalis*, were encountered on the sand flat. *Holothuria atra* was fairly common, with a population density of 0.83 ± 0.34 (s.d. = 2.92) across stations 7-9 (to where it was limited to) on the sand flat. *Bohadschia vitiensis* is common at the lagoonward margin of the sand flat at low intertidal to shallow subtidal depths where it partially burrows in the sand bottom. Bolton (1982a) recorded eight species of holothurians from the sand flat, four at densities of up to several hundred per square meter; reconciling her data with the present findings is difficult.

An unidentified zoanthid (probably a *Zoanthus* species; cf. Muirhead & Ryland, 1993) covers large patches of the sand flat in some areas but is rare or absent in others. Zoanthids were encountered in four of the seven transects in which they were consistently sampled, and were limited to Stations 5-9 on these transects (mid-sand flat to lagoon-slope margin) (Fig. 7). Bolton (1982a) found them in two of her six transects, and again found them limited to the lagoonward two-thirds of the sand flat. Zoanthid cover was consistently high (25 ± 5.6 %; across stations 5-9) in the three transects situated in the Abarao-Eita area, but low (0.47 ± 0.47 %) in the four transects situated west of there. Zoanthids dominated Bolton's (1982a) Bairiki and Teaoraereke transects in this western area.

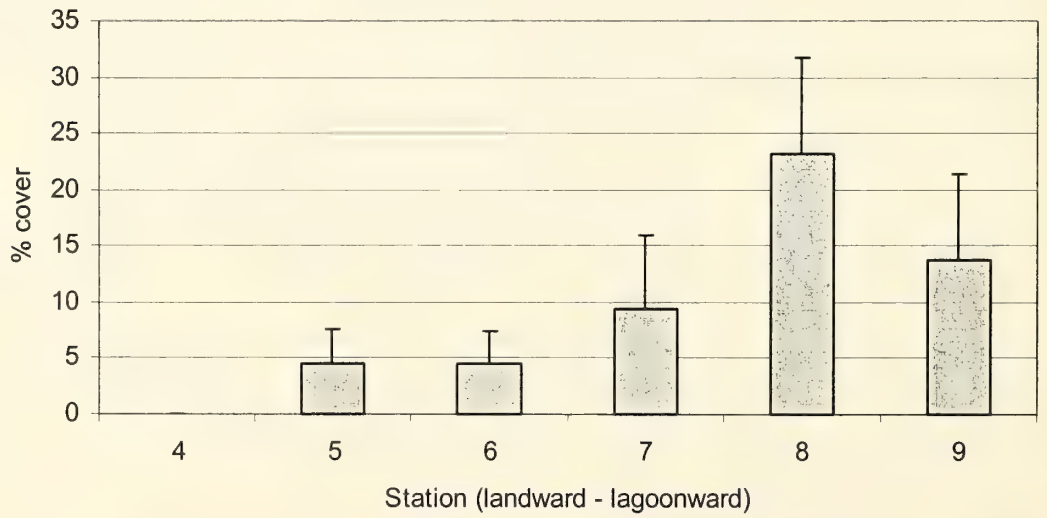

Figure 7. Mean percent cover (± SE; among seven transects with zoanthid data) of zoanthids across South Tarawa sand flat from nearshore to lagoonal slope margin (Stations 4-9)

Overall, zoanthids covered 11 ± 3% of the sand flat averaged across all transects where they were measured in South Tarawa (Stations 5-9). Cover was highest in the Abarao-Eita seagrass beds (Station 7-9 in 3 transects) where 36 ± 8% of the bottom was covered by zoanthids. At such a high abundance, zoanthids must have an important effect on the benthos, especially in combination with high seagrass cover. They may limit access to

the sediment or water column, may affect recruitment by feeding on larvae of infaunal organisms, and stabilize the sediment. Nevertheless, abundant shellfish occur in such dense zoanthid beds.

Lysiosquilla maculata (*te varo*), the world's largest stomatopod (to 38.5cm; Manning, 1978), is common along the lagoonward margin of the sand flat, and is the focus of a specialized local fishery. The abundance of this species was not measured, but burrows are spaced a few meters apart on the outer sand flat around lowest low water. *Te varo* fishing is a skill practiced by few families (B. Yeeting, pers. comm.). I observed one fishing party harvesting this spectacular animal. Each fisher inserted a bait (a small pufferfish, used because its tough skin makes it reusable), tied by a length of coconut senit to half a coconut shell (serving as anchor), into a *te varo* burrow. The bait was then left for a couple of minutes after which the line was felt for the activity of the stomatopod. If the animal was feeding, it was slowly teased out of its burrow by pulling the bait back up, and swiftly grabbed at the burrow entrance. This teasing-out process apparently requires much skill and there was considerable variation in success among the fishers. The animal is grabbed with one hand when it is still mostly in its burrow, then grabbed at the abdomen with the other hand as it is slowly pulled out of the burrow. The notorious armature of the uropods is then bitten off, making the animal safer to handle. According to Being Yeeting (pers. comm., based on Yeeting's discussion with *te varo* fishers) these stomatopods live in pairs with the males doing all the prey capture; thus males are readily caught. After catching a male, the fisher marks the burrow and comes back in a couple of days to catch the by-then-famished female, using the same method.

Lagoon Slope

The lagoon slope, as here defined, begins at the outer edge of the seagrass bed at approximately 0.5 m depth at lowest low water. It slopes gently to a depth of about 8-10 m, about 1 km from the sand-flat margin in South Tarawa. *Anadara* beds on the lagoon bottom were encountered only on this marginal slope along the eastern section of South Tarawa (Fig. 1), within 1 km of the sand-flat margin, lying largely at depths of <8 m. The bottom of this area is composed of silty sand and usually has a pronounced crater and mound topography created by the infauna with 10-20 cm vertical relief.

The most abundant species encountered in both surveys of the lagoon slope were the heart urchins *Maretia planulata* and *Metalia sternalis,* the sand dollar *Laganum depressum*, and the mollusks *Anadara uropigimelana* and *Strombus luhuanus* (Table 1). Among smaller species, the gastropods *Turritella cingulifera* and *Strombus erythrinus* were abundant and the minute irregular echinoid *Fibularia* sp. common, although these species were not consistently sampled.

The distribution of these five species is patchy, with one or a few often dominating in patches of tens of meters or more across. The domination of the epibenthic *Laganum* and *Strombus* are especially conspicuous, although the infaunal species are also patchy. *Anadara* is largely confined to a few well-defined beds (see below).

Table 1. Population density (m^{-2}) of dominant macrofauna in quantitative surveys of lagoon slope in South Tarawa.

Survey	*Anadara*	*Strombus*	*Laganum*	*Maretia*	*Metalia*	All echinoids
Transect	4.8 ± 1.7	5.3 ± 1.9	11 ± 3.0	23 ± 4.3	8.5 ± 1.1	43 ± 6.0
Bed	15 ± 2.6	10 ± 3.2	19 ± 4.4	12 ± 1.9	7.2 ± 1.1	38 ± 5.1
Combined	7.8 ± 1.2	6.7 ±1.7	13.5 ± 2.5	20 ± 3.1	8.1 ± 0.9	42 ± 4.2

Transect = data from transect survey along length of South Tarawa lagoon slope ($N = 90$ quadrats)
Bed = data from survey of Tangintebu-Bangantebure *Anadara* bed ($N = 40$ quadrats)
Combined = combined data from the above two surveys.
Echinoids = combined data for three irregular echinoids. *Strombus* is *S. luhuanus* only.

Anadara uropigimelana

The survey along the length of the South Tarawa lagoon slope showed that offshore *Anadara* populations were localized to one large and a couple of small beds. *Anadara* was absent from most stations and some entire transects, but was abundant at a couple of sites, thus showing great overall variation in population density (4.8 ± 11.1 m^{-2} s.d.; $N = 90$ quadrats). No *Anadara* were found on two transects, and mean density was >2 m^{-2} on only four of the nine transects. The well-known Tangintebu-Bangantebure *Anadara* bed was traversed by two transects (#6 and #7), and these encountered *Anadara* at all stations except the one closest to land. In contrast the other five transects that encountered *Anadara* found the clams only at one of the four stations sampled, implying that the patches encountered were small. Two of these transects (#3 and #4) encountered *Anadara* at high (26-42 m^{-2}), and three (#5, #8 and #9) at low (2-10 m^{-2}) densities. Furthermore, in three of these transects (#3, #8, and #9), *Anadara* were encountered only at the nearshore station located only 90 m from the margin of the sand flat. These may represent extensions of the sand-flat beds rather than be independent slope *Anadara* beds. The results thus support the hypothesis that the only large *Anadara* bed on the lagoon slope is in the Tangintebu-Bangantebure area, although a few small beds exist elsewhere.

Spot surveys of the Tangintebu-Bangantebure *Anadara* bed showed that it extends for ca. 4.6 km (ca. 173°03.2'E to ca. 173°05.7'E) and is 640 ± 210 m wide (s.d.; $N = 4$ transects, range: 420-900 m wide), encompassing a total area of 2.9 ± 0.5 km^2. Within this area, spot checking revealed that *Anadara* was sufficiently abundant at 87% of the sites ($N = 30$) to be visually apparent within one to three free dives. It was also present at all 10 stations haphazardly selected for sampling within the bed and occurred in 90% of the 40 quadrats surveyed at these stations (Fig. 8). The few sites in the survey where no *Anadara* was seen appeared to be off the bed; adjacent landward or lagoonward sites always supported the shellfish. Thus, *Anadara* appears to form a single, largely contiguous bed in this region.

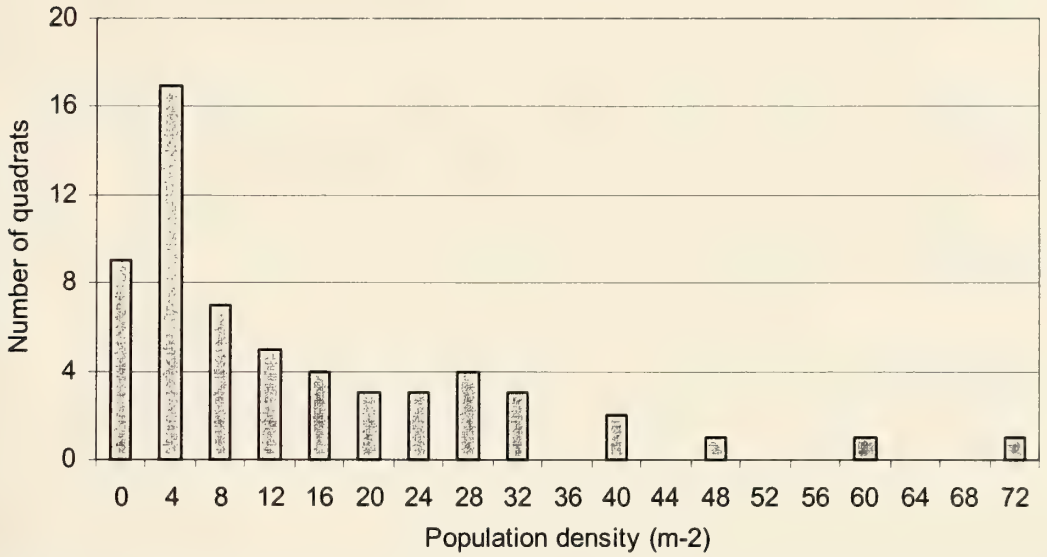

Figure 8. Frequency distribution of per-quadrat population density of *Anadara uropigimelana* within Tangintebu-Bangantebure bed in Tarawa Lagoon. Based on combined data from *Anadara* bed survey and transects six and seven (which traversed the bed) of the transect survey (n=60).

There is considerable variation in population density within this *Anadara* bed (Fig. 8). Part of this variation is likely due to human harvest. Free divers focus their attention on the densest beds and probably find that moving on, before an area is completely exhausted, is economically advantageous (see below).

The two surveys yielded similar estimates of population size for offshore *Anadara*. The transect survey along the 15 km long, 1 km-wide-lagoon slope yielded an estimated abundance of $7.2 \pm 2.6 \times 10^7$ clams. The survey of the Tangintebu-Bangantabure *Anadara* bed yielded an estimated abundance of $4.4 \pm 1.6 \times 10^7$ animals in this bed. Note that both surveys focused only on large (>2cm) *Anadara*.

Strombus spp.

The patchy distribution of the two abundant *Strombus* species, *S. luhuanus* and *S. erythrinus*, is strikingly apparent on dives over the lagoon slope; a third species, *S. variabilis*, is less common. Mature and juvenile *S. luhuanus* and *S. erythrinus* tend to aggregate and segregate by species, and *S. luhuanus* also by maturity. Thus, in any given area, either *S. erythrinus* or mature or juvenile *S. luhuanus* dominate. *Strombus luhuanus* tends to be most common where exposed rubble is present, probably because it feeds on benthic macroalgae that attach to rubble. In contrast, *S. erythrinus* feeds on the red alga *Grateloupia* that lies on the sand in large (typically 10-50 cm), loose, or poorly attached, fluffy masses.

Strombus luhuanus had a mean density of ca. 7 m^{-2} (combined surveys, with comparable densities in both) (Table 1). Like *Anadara*, *S. luhuanus* is restricted to the marginal ca. 1 km-wide portion of the lagoon bottom. Along the 15 km-stretch survey the abundance of this conch was $8 \pm 1.7 \times 10^7$, while an estimated $2.9 \pm 1.0 \times 10^7$ occurred within the Tangintebu-Bangantabure *Anadara* bed. *Strombus erythrinus* and *S. variabilis*

were counted regularly only in the *Anadara* bed surveys, where densities were 8.5 ± 2.2 m^{-2} and 1.1 ± 0.4 m^{-2}, respectively.

The occurrences of *Anadara* and *S. luhuanus* were significantly associated ($P < 0.0001$, G test, combined data from both surveys) and although *S. luhuanus* occurred in only 28% of the quadrats, it co-occurred with *Anadara* in 89% of them. The mean density of irregular echinoids was somewhat, but not significantly, lower (32 versus 50 m^{-2}) in quadrats where *Anadara* occurred, compared with those where the clam was absent.

Two hypotheses could explain this association between a benthic algal grazer and a suspension feeder:

1) *Anadara* needs hard substrata (rubble or adult shells) for attachment when young, whereas *S. luhuanus* feeds on benthic algae, which also need hard substrata for attachment. Thus, the correlated abundance of these shellfish may be a function of the availability of exposed hard substrata. *Anadara* beds may themselves create such a habitat by littering the bottom with their abundant dead shells, which are suitable for algal attachment as well as for the attachment of young clams.

2) The abundance of both species may correlate negatively with that of irregular echinoids and thus they may congregate at the few sites where irregular echinoids are uncommon. Irregular echinoids bulldoze soft bottoms and can greatly influence small infaunal organisms (Highsmith, 1982). Even if such disturbance does not affect adults of these two mollusks, it may negatively influence recruitment. The relatively weak correlation between the density of irregular echinoids and mollusks, however, speaks against this hypothesis.

Other Species

Fishes were uncommon on the open sandy expanse of the lagoon slope, although stingrays were occasionally seen. However, small acanthurids, lutjanids, serranids, occasional balistids, and other reef fish hovered around the scattered bits of reef. Patch reefs on the lagoon slope were mostly <2 m across and were comprised largely of *Porites*. *Pocillopora damicornis* was the only other coral seen in the fringing patch reefs of the southeastern lagoon, although off Betio *Montipora* and *Acropora* were also common (Zann and Bolton, 1985). Areas around these small patch reefs were densely strewn with shells, especially of *Anadara*, apparently gathered by predators. Some of the shells had been crushed near their posterior end, indicating possible attack by triggerfishes; others were intact.

Lagoon Floor

The lagoon floor is a relatively flat plain, mostly 5-20 m deep (25 m max.; Bolton, 1982a), that stretches between the intertidal sand flat and the submerged western barrier reef and includes the lagoon slope just considered. Numerous patch reefs and shoals rise above the plain of the lagoon floor (Fig. 1). Although no significant invertebrate resources are taken from the lagoon floor, a limited survey was conducted to characterize its biota.

The lagoon floor exhibits marked west-to-east and north-to-south gradients in most variables, including the nature of benthic habitat, species composition, and abundance of mollusks and echinoids. Sediment grain size (Weber and Woodhead, 1972; Richmond, 1990) and coral cover and diversity decreased markedly from north to south and west to east. While only occasional *Porites* and *Pocillopora damicornis* colonies were noted on the southern transects, diverse coral communities were encountered on the much coarser, gravelly sand bottoms of the northwestern and west-central stations. This trend in northwesterly increasing coral diversity and abundance was also observed and quantitatively documented on the patch reefs and shoals (Paulay and Kerr, 2001).

Three species of medium-sized (ca. 5 cm max. test length) irregular echinoids (*Laganum depressum*, *Maretia planulata*, and *Metalia sternalis*) dominate large areas of the inner (i.e. southeastern) lagoon floor, while mollusks, except for a few small species (see below), are uncommon and constitute only a small fraction of the biomass in this area. The minute irregular echinoid *Fibularia* sp. also appears to be very abundant. The distribution of these three echinoids is closely related to the distribution of sedimentary facies (Fig. 9).

Maretia planulata is the most abundant, and also the most striking, species in the deeper inner lagoon. While this echinoid is infaunal on sandy bottoms, it becomes strictly epifaunal on muddy bottoms, apparently unwilling to burrow into such fine sediments. On muddy bottoms this species tends to occur in huge "herds", often with population densities well in excess of 100 m^{-2}, providing a striking sight as they move around on top of the mud with the aid of their elongated spines. This species was encountered at all seven stations (in 12 of 14 quadrats) in the southeastern lagoon, at a mean density of 55 ± 18 m^{-2} (Fig. 9). Within this area, the abundance of *M. planulata* was correlated with sedimentary facies. Densities were much higher at the four stations in the sandy mud facies (88 ± 27 m^{-2}) than at the three stations in the silty sand facies occupied by these echinoids (10.7 ± 3.2 m^{-2}) (Fig. 9). *Maretia* was absent from all seven stations in the northwestern lagoon.

Laganum depressum was also limited to the southeastern lagoon where it was encountered at the nine southeasternmost stations (Fig. 9) at a mean density of 3.6 ± 1.7 m^{-2}. In contrast, it was absent from the five stations to the northwest. *Metalia sternalis* was the most widespread species; it was ubiquitous (encountered in 19 of 20 quadrats) through the mid- and eastern-lagoon at a mean density of 13.5 ± 2.2 m^{-2}, but was absent at the four western stations (Fig. 9).

Thus, the distribution of all three echinoid species is limited largely to lagoonal bottoms with a high silt fraction. The combined density of these three species is significantly higher among stations located within the sandy-mud facies (116 ± 27 m^{-2}, 4 stations) than in the silty-sand facies (4 ± 1.8 m^{-2}, 8 stations) (ANOVA, $p < 0.001$).

We found only a few species of mollusks on the silty and muddy bottoms of the southeastern lagoon. A small (ca. 5 mm), unidentified, transparent tellinid bivalve was the only abundant infaunal species living even in the finest lime mud. The turritellid gastropod *Turritella cingulifera* occurred in large epibenthic aggregations while the skeneid gastropod

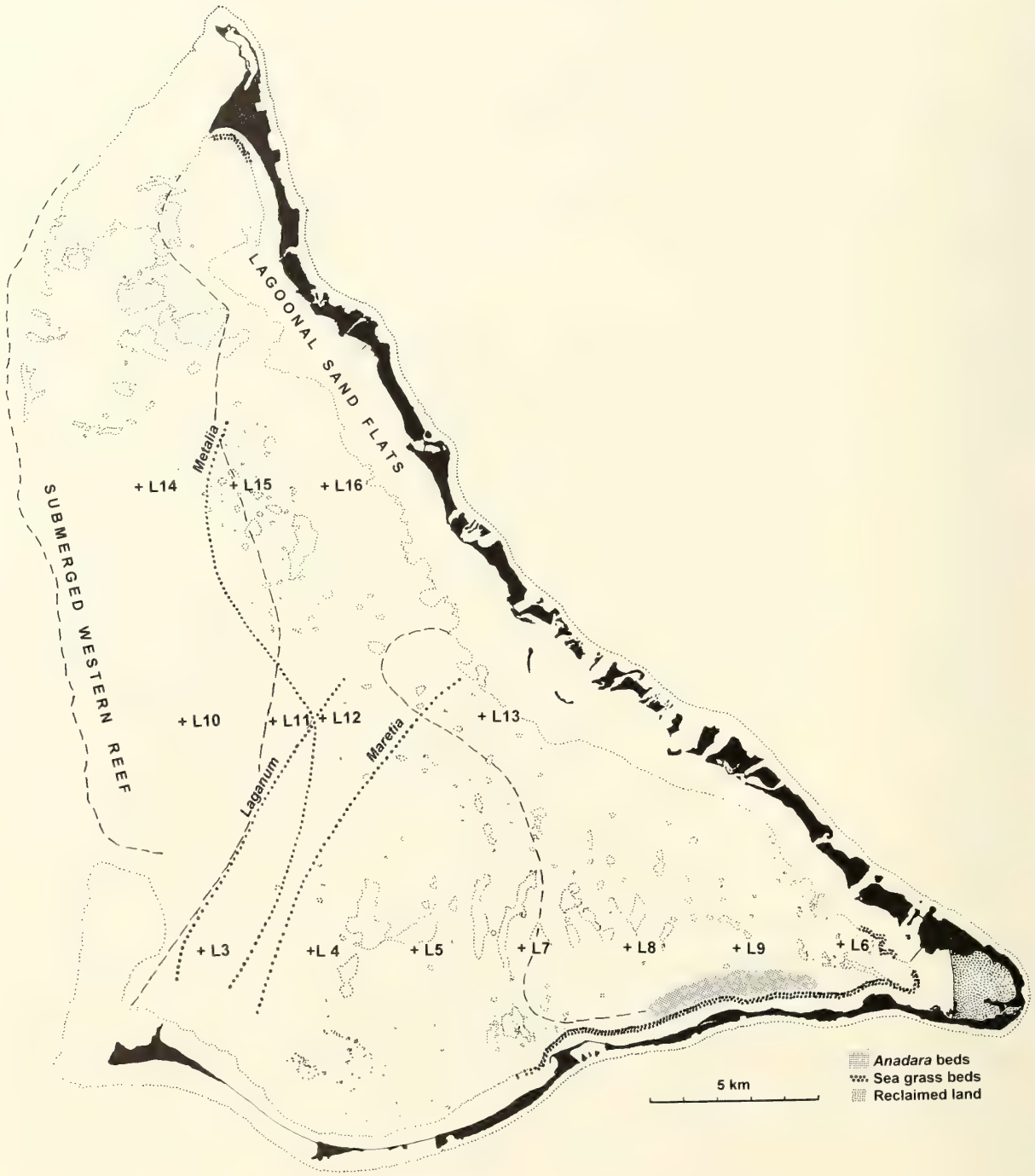

Figure 9. Lagoon bottom of Tarawa. Dashed lines traversing lagoon delineate three major sediment facies: gravelly sand, silty sand and sandy mud (west to east) (after Richmond, 1990). Dotted lines mark western distributional boundary of three irregular echinoids (*Maretia planulata, Metalia sternalis, Laganum depressum*) within the lagoon; each species was encountered at all lagoonal stations southeast of, and at none northwest of, lines. Locations of 14 lagoon-bottom stations indicated by L3 - L16 (see Appendix I for coordinates). True north toward top of page.

Cyclostremiscus cingulifera was fairly common cruising on top of the mud. The naticid gastropod *Tectonatica robillardi* was also fairly common. Dead mollusk shells occurred in much higher diversity then living mollusks. Although this in part may be the result of a sampling artifact caused by the relative rarity of larger species together with the durability of their shells, it may also reflect temporal changes in lagoon-floor mollusk assemblages. The presence of vast quantities of empty shells but no living individuals of several small, fragile species (e.g., *Musculus* sp., perhaps the most common mollusk shell on the lagoon floor) indicates that these species were much more abundant at some time in the past than today. This trend may reflect periodic, short-lived blooms of certain species or the gradual, long-term turnover of bottom communities (cf. Holocene turnover in lagoon-bottom mollusks in Enewetak Atoll, Kay and Johnson, 1987; Paulay, 1991).

Unlike the shallow-water habitats in the lagoon, the deeper lagoon floor (but not the lagoon slope, see above) supports few shellfish resources. Lagoon floor communities differ in species composition from shallow (shoal and sand-flat) communities, sharing only a few species. Most of the heavily exploited species of the sand flat are absent or rare on the lagoon floor. Thus, the lagoon floor does not hold important brood stock that could supply overexploited sand-flat populations with recruits.

The only economically important species encountered regularly on the lagoon floor was *Anadara uropigimelana*, apparently a fairly eurytopic animal. Nevertheless, although occasional shells of this species were found at many sites, no living specimens were encountered in the lagoon bottom surveys indicating that this species is not common on the lagoon floor. High population densities of *S. luhuanus* were encountered on the slopes and tops of numerous patch reefs and shoals; however, this species appears to be essentially absent from the plain of the deeper lagoon floor.

Gatherer Surveys

Sand Flat

Tidal height and day of the week strongly influence gathering effort. Time constraints prevented a thorough assessment of how these variables affect the number of gatherers on the sand flat, as only six gatherer counts were made (Table 2). Nevertheless, a rough estimate of gathering pressure can be made. On a Saturday with a relatively low tide (LW 0.2 m, 12 February 1994), 691 people were observed gathering within a 3-hour period centered around low tide. Given that many people collect for only 1-2 hours, many gatherers likely were missed during the drive-through spot checks. An estimated 1,000 people may have been gathering on that day. On a Monday with a moderately low tide (LW 0.5 m, 14 February 1994), 303 people were counted gathering within a 2-hour period centered around low tide and an estimated >400 people likely gathered shellfish that day. Thus, about twice as many people gather shellfish on Saturdays than on weekdays. In contrast, 60 people were counted on the Sunday (LW 0.3 m, 23 February 1994) between these days, indicating that gathering on Sundays is minimal. The height of low water also clearly makes a difference because little gathering activity occurs on days with relatively high low tides (26 people were counted on 19 February 1994, tide 0.9-1.2 m).

Table 2. Number of shellfish gatherers counted on South Tarawa sand flat.

		Low Tide		Survey Time		
Date (1994)	**Day**	**Height**	**Time**	**Start**	**End**	**Count**
2 February	Friday	0.2	10:53	11:50	14:00	148
12 February	Saturday	0.2	11:24	10:40	13:20	691
13 February	Sunday	0.3	11:52	11:20	13:00	60
14 February	Monday	0.5	12:18	11:30	13:15	303
19 February	Saturday	~1.0	17:39	14:25	15:50	26
22 February	Tuesday	0.6	07:45	08:10	09:20	112

The 19 February count was not taken during low tide. Tides changed from 1.2 m at 10:34 to 0.9 m at 17:39 on that day.

Thus the increase in gathering activity on Saturdays roughly cancels out the greatly decreased gathering activity on Sundays. Assuming an average daily gathering population that fluctuates between 500-1,000 during the best low tides and 0-100 during the poorest tides, with a mean of perhaps 200-400 people per day, yields ca. 75,000 - 150,000 person-days on the sand flat of South Tarawa per year. The mean catch of gatherers on the sand flat was 7.6 ± 0.5 kg person^{-1} effort^{-1} (N = 124) (Fig. 10). Thus, about 600-1,200 tons of shellfish are taken per year by people gathering on the sand flat.

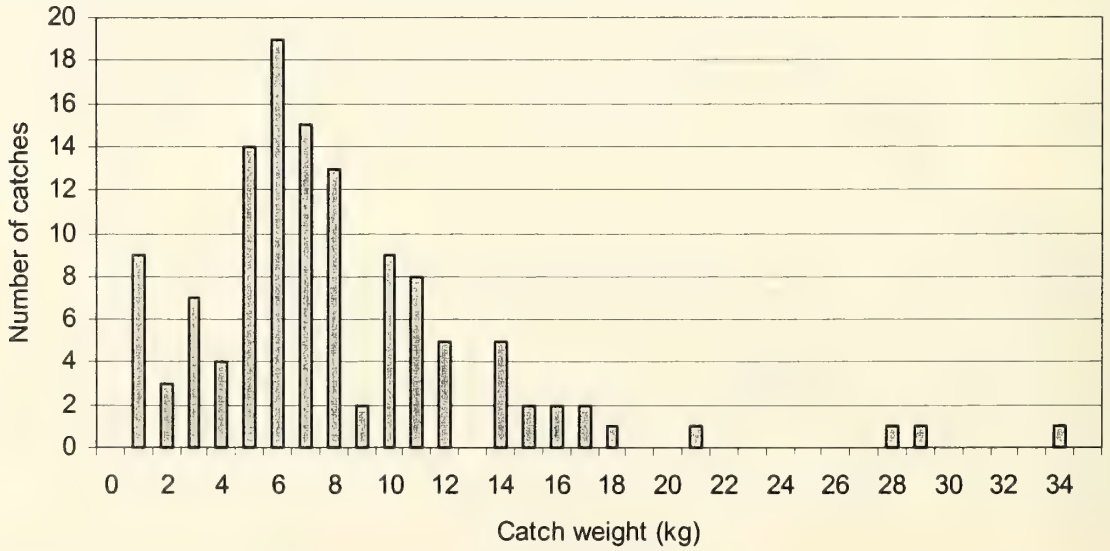

Figure 10. Frequency distribution of catch-per-person effort for shellfish gatherers working South Tarawa sand flat. Mean ± SE: 7.6 ± 0.5 kg. The weight of catches made by parties of >1 gatherers was divided equally among members of the party. N = 124 samples based on N = 96 landing parties.

A total of 19 species was identified in the catches sampled (Fig. 11). Gatherers appear to consume all shellfish species of sufficient size (>ca.1 cm) and many mollusks have common names (Appendix II), suggesting their importance as food.

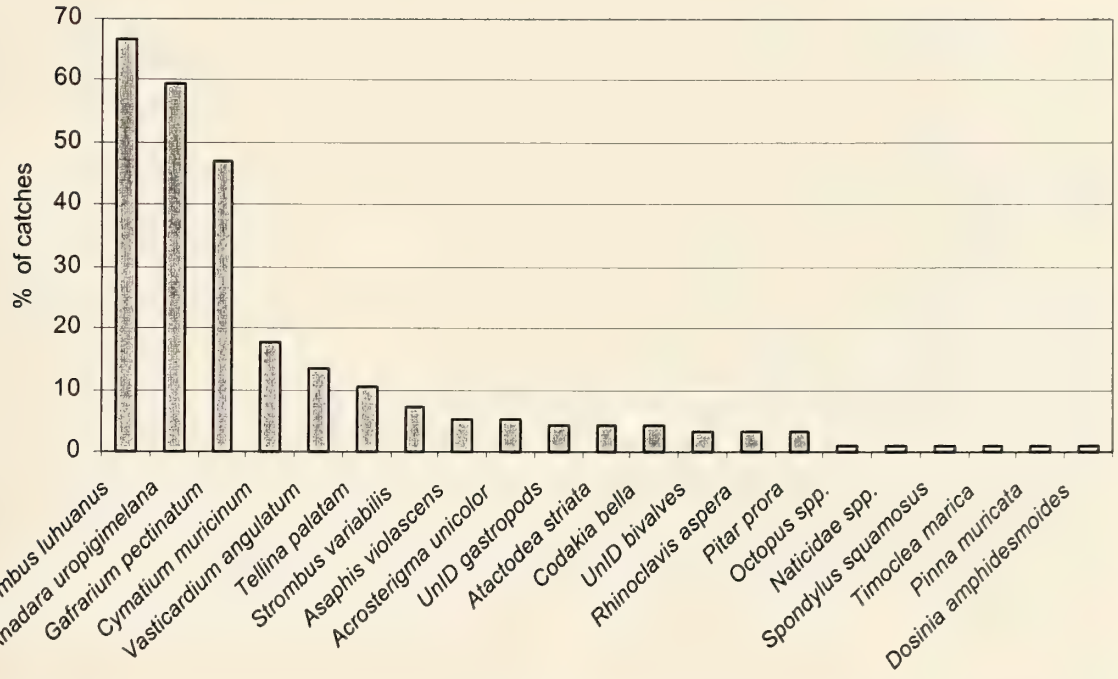

Figure 11. Percentage of catches in which named species were found among all surveyed landings ($N = 96$) from South Tarawa sand flat.

Strombus luhuanus, *Anadara uropigimelana*, and *Gafrarium pectinatum* were by far the most common species in the catches examined, occurring in 67%, 59%, and 47% of the catches ($N = 96$) respectively (Fig. 11). Most (91%) catches were dominated (defined as constituting >75% of catch weight) by one of four species (Fig. 12), most commonly *S. luhuanus* (55% of catches), and *Anadara* (24% of catches). The other catches were not dominated by single species.

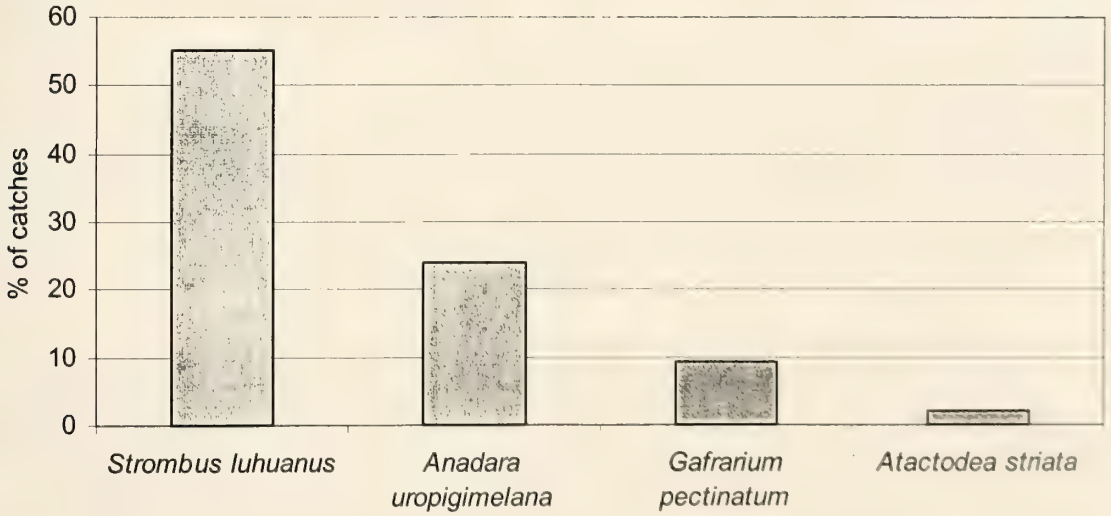

Figure 12. Dominant species in catches from Tarawa lagoon. Percentage of all gathering catches that were dominated (defined as constituting >75% of weight of catch) by single species.

The mean total weight of *S. luhuanus* in each catch in which it occurred was 8.1 ± 1.0 kg, with a value of 8.6 ± 1.2 kg for *Anadara* and 1.2 ± 0.3 kg for *Gafrarium*. These weights are probably slightly overestimated because better species-specific data were available for catches dominated by single species than for catches of mixed species. Nevertheless, they should not be biased against particular species. Multiplying incidence in catch with weight per catch therefore indicates that the three dominant species were taken at a ratio of 5.4 : 5.1 : 0.6 (*S. luhuanus* : *Anadara* : *Gafrarium*). Assuming that these three species constitute about 90% of the total catch, they constituted approximately 44%, 41%, and 5%, respectively, of the South Tarawa-wide sand flat shellfish catch. Given that about 900 tons (see above) of shellfish are harvested, the yearly harvest would be approximately 400 tons of *S. luhuanus*, 370 tons of *Anadara*, and 45 tons of *Gafrarium*. Divers (see below) take an additional 1,000 tons of Anadara. On the basis of a household survey, Bolton (1982b) estimated that about 1,730 tons of *Anadara*, 850 tons of *S. luhuanus* and 280 tons of *Gafrarium* were taken in South Tarawa in 1982. She also noted, however, that the nature of her survey likely leads to an overestimate of the true harvesting pressure.

The mean weight of *S. luhuanus* individuals was 10.5 ± 0.52 g (mean ± SE in $N = 17$ harvests; s.d.= 2.2 g), of *Gafrarium* was 7.5 ± 0.46 g ($N = 15$ harvests; s.d.= 1.8 g), and of *Anadara* was 20 ± 2.5 g ($N = 26$ harvests; s.d.= 13 g). The low variance in *S. luhuanus* weight reflects that only large juveniles and adults of this species with determinate growth are taken. In contrast, the higher variance in *Anadara* weight reflects the great variability in this species' size among beds caused largely by irregular recruitment (see Tebano and Paulay, 2001). Thus, intense recruitment in the southeastern "elbow" started a new *Anadara* fishery in 1993. Those taken in this area in early 1994 averaged 6 ± 0.8 g (mean ± SE in $N =$ 8 harvests) compared with 26 ± 2.6 g ($N = 18$ harvests) for *Anadara* taken elsewhere.

Given these average weights, the yearly harvest tonnage estimated above translates to approximately 4×10^7 *S. luhuanus*, 2×10^7 *Anadara*, and 6×10^6 *Gafrarium* taken from the South Tarawa sand flat. These values are comparable to the rough abundance estimates of these species on the sand flat (see above) of 7×10^6 *S. luhuanus*, 6.3×10^6 *Anadara*, and 6.6×10^7 *Gafrarium*. The disparity between the estimated *Anadara* density and the higher annual harvest is partly a result of the immense recruitment event in the southeastern elbow (see Tebano and Paulay, 2001) that contributed to the harvest of that species in 1994 when much of the harvest data were collected. This event had not yet occurred when the sand flat populations were surveyed in 1992. Nevertheless, these estimates indicate that the harvest of *Anadara* is close to, if not in excess of, its rate of production.

As noted above, the abundance of *S. luhuanus* was probably underestimated but offshore refuges protect *S. luhuanus* populations from overharvesting. This species was abundant in most shallow-water habitats surveyed in the inner lagoon, ranging from the low intertidal zone to ca. 8 m depths. Poiner and Catterall (1988) also found this conch common to a depth of 9 m in Papua New Guinea. The abundance and age structure of this species varies greatly. Although our quantitative surveys encountered it almost exclusively at low densities, *S. luhuanus* is extremely abundant (>50 m^{-2}) in many areas not quantitatively surveyed, especially on the lower slopes of shoals. Juveniles and adults are commonly found

in separate aggregations; similar aggregations are well known elsewhere (Poiner and Catterall, 1988). These aggregations probably are behavioral because aggregations of different age classes are often found near each other, well within the crawling range of this highly mobile gastropod.

Although the harvesting pressure on the sand flat on *S. luhuanus* is high, large aggregations on the lagoon slope, accessible only by diving, and those on shoals, accessible only by boat, are virtually unfished. The bulk of this conch's stock is in these refuges. Catterall and Poiner (1987) suggested that this species is capable of migrating to shallow water. Migrants from deep water may continually replenish the *S. luhuanus* populations on the sand flat although we have no data to test this hypothesis. Nevertheless, such migration could also explain the discrepancy between sand-flat stock and harvest estimates. In Papua New Guinea, deep-water populations, together with the frequent burial of juvenile stages, offer this species refuge from overexploitation (Poiner and Catterall, 1988). In contrast, *S. luhuanus* populations have been decimated by overharvesting in the Ryukyus (Yamaguchi pers. comm.). The species forms the basis of artisanal fisheries throughout much of its range. *Strombus luhuanus* has separate sexes and determinate growth. Population studies conducted in Papua New Guinea show that this species reaches sexual maturity at about two years of age (Poiner and Catterall, 1988).

On Tarawa, *G. pectinatum* appears to be almost ubiquitous on the intertidal sand flat and many lagoonal shoals but it is rare or absent in reef areas of the western lagoon. Except in Temaiku, this species is rarely the focus of collecting in South Tarawa; it is, however, an important bycatch. Its offshore populations, large population size, and probable rapid growth rate protect this resource. *Gafrarium pectinatum* is harvested in many areas across its wide Indo-West Pacific range, including many Pacific islands. In Hong Kong, Morton (1990) showed that the species has separate sexes, matures at one year of age at a size of 16-20 mm, and lives up to three years, reaching a maximum length of just over 35 mm. It reproduces at a low level throughout the year but has a seasonal peak during spring and fall in that seasonal climate.

Because the survey of gatherers on the sand flat was set up around the lowest tides, it virtually ignored gathering activity focused on the bivalve community of the beach slope, a habitat that is accessible in all but the highest tides. We have frequently observed people gathering in this habitat, collecting the bivalves *Asaphis violascens* (*te koikoi*) and, to a lesser extent, the much smaller *Atactodea striata* (*te katura*). While *Asaphis* is clearly a favored shellfish, *Atactodea* is taken mostly incidentally, or for baby food (so noted by informants), because of its small size. Because *Asaphis* inhabits a zone accessible even on the worst tides, it is a valuable resource for subsistence gatherers. It is generally shunned on beaches adjacent to villages, however, because the population uses *Asaphis* habitat for toilet purposes. All the observed gathering of this species occurred along causeways or in front of the hotel, areas not regularly used for defecation. Although the narrow zonation of *Asaphis* in an accessible habitat makes it vulnerable to overharvesting (Catterall and Poiner, 1987), much of its habitat is in areas shunned by collectors, providing a refuge for the species. The size range of harvested *Asaphis* in South Tarawa, however, appears to be well below the

maximum size attained by the species, perhaps as a result of overharvesting. The abundance of the species, however, implies abundant recruitment.

The actual importance of *Asaphis* as a shellfish resource is unclear. No *Asaphis* collectors were encountered in the gatherer surveys, although I have seen people collecting this species on several other occasions. The importance of *Asaphis* relative to *Anadara, S. luhuanus,* and *Gafrarium* appears to be minor. In contrast, on the basis of a household survey, Bolton (1982b) estimated that about 464 tons of *Asaphis* were harvested throughout North and South Tarawa in 1982. She also noted, however, that the nature of her survey probably leads to an overestimate of the true harvesting pressure. Bolton's estimates for *Asaphis* harvesting may also be excessive because the indigenous name for the species, *te koikoi*, is often inappropriately applied to a wide range of shellfish today.

Offshore Anadara Beds

Anadara is frequently harvested by divers on the lagoon slope at depths of 2-8 m. To work in this area, divers need a vessel to hold their catch. A variety of vessels are used, including floats (made from rubber inner tubes fitted to hold bags of *Anadara,* which are the most common vessels), outrigger canoes, and aluminum dinghies; some dinghies are fitted with outboards and some canoes with sails.

Counts of divers on the Tangintebu-Bangantebure *Anadara* bed are much more accurate than counts of gatherers on the sand flat, partly because of the small size of the area, as well as of the gatherer population, and the visibility of harvesters on the water. Counts were made on 6 days: 3 during the early afternoon, when more than 90% of the divers were likely onsite, and three during the late morning, when some divers had not yet arrived. An average of 34 divers worked these beds on the 3 days when counts were made in the afternoon (Table 3).

Table 3. Results of survey of divers collecting *Anadara* from offshore beds.

Date (1994)	Time	Number of Vessels	Number of Divers	Divers per Vessel[1]
15 February	11:00	14	25	1.79
17 February	10:45	9	17	1.89
18 February	11:15	15	27[2]	
21 February	13:00	21	35	1.67
22 February	13:30	17	30	1.76
23 February	13:00	21	38	1.81
Mean ± sd[3]		**16.2 ± 4.6**	**28.6 ± 7.5**	**1.8 ± 0.1**
Mean ± sd[4]		**19.7 ± 2.3**	**34.3 ± 4.0**	**1.8 ± 0.1**

[1]Divers per vessel = calculated mean number of divers per vessel.
[2]Not counted, estimated from divers per vessel ratio
[3]Mean of all values.
[4]Mean of 21, 22, and 23 February, when surveys were conducted during peak gathering times.

Divers pack their *Anadara* catch into standard-sized rice bags that hold 34 ± 1.5 kg per bag (s.d.; $N = 5$). Interviews indicated that the average diver takes 3.3 ± 1.6 bags per day (s.d.; $N = 10$). Thus, the diving fishery lands about 3800 kg of *Anadara* per day. Considering that little gathering occurs on Sundays and that gathering during stormy weather is not possible, divers gather on perhaps 275 days per year, with an estimated yearly harvest of about 1,000 tons. Given that the large offshore *Anadara* have an average weight of ca. 50 g, this annual harvest weight translates to a harvest of 1.6×10^7 *Anadara*. With an estimated population of 4.4×10^7 clams in the Tangintebu-Bangantebure bed, or 7.2×10^7 clams in the entire South Tarawa lagoon slope (see above), this figure represents a harvest of about one-third to one-fifth of the total adult population per year.

The growth rate of *Anadara* in Tarawa Lagoon is not well documented, but preliminary data indicate that the typically harvested 3-6 cm shellfish must be at least 2-3 years old. Recruitment of the species appears to be episodic, being highly variable in both time and space (Tebano and Paulay, 2001). Thus, the harvests in the offshore beds are near to, if not exceeding, sustainable rates.

In contrast to gathering shellfish on the sand flat, a practice primarily motivated by subsistence, diving for *Anadara* is a commercial venture, with 80% of the interviewed divers ($N = 10$) collecting *Anadara* for sale. These divers routinely collect *Anadara* 6 days a week (which is one reason for the low variance in the number of people seen collecting per day). With a bag of *Anadara* selling for A $6 on the roadside (February 1994; A$5 in 1993), they earn ca. A$20 per day, a good wage by Tarawa standards. Although this venture is lucrative, the *Anadara* populations may not be able to support much expansion in harvesting. However, the strenuous nature of harvesting limits over harvesting of offshore *Anadara* beds. Collectors free dive to 3-6 m for many hours each day. Divers search for areas with high *Anadara* densities where they can grab numerous clams on each dive. Divers avoid portions of the bed with lower shellfish density, so once density becomes moderately reduced, harvesting becomes unprofitable, providing a refuge for the shellfish.

SUMMARY AND CONCLUSIONS

The abundance of benthic macroinvertebrates in Tarawa Lagoon is striking and unusual. Oceanic atolls typically support a relatively low abundance and biomass of macrobenthos. The major exceptions to this trend are "closed" atolls where water exchange with the surrounding ocean is limited and the residence time of lagoon waters can be several weeks to months. The lagoons of closed atolls tend to have low-diversity faunas dominated by one or a few extremely abundant species of high biomass (Salvat, 1969). Frequently, the dominant species are photosymbiotic bivalves, which derive much of their nutrition autotrophically. Thus, giant clams (*Tridacna maxima*) are abundant in several closed atolls (e.g., Reao, Takapoto, Vahitahi [Tuamotu], and Caroline [Line]) and the photosymbiotic cockle *Fragum fragum* is extremely abundant on the sand flats of others (e.g., Anaa and Tuamotu) (Salvat, 1969, 1972; Richard, 1977, 1982; Sirenko, 1991). Some closed atolls also host abundant heterotrophic bivalve populations, especially the epibenthic species *Arca ventricosa, Pinctada maculata,* and *Chama iostoma* (Salvat, 1969; Richard, 1978, 1985a, b).

These latter species presumably subsist on the relatively high, indigenous lagoonal productivity of closed atolls (cf. Sournia, 1976; Delesalle, 1982).

In contrast to the macrobenthos of typical closed atolls that are characterized by low diversity and high biomass and the macrobenthos of typical open atolls that are characterized by high diversity and low biomass, Tarawa hosts high diversity and high biomass in an open lagoonal setting. With the entire western side submerged, the residence time of lagoonal waters is about one week (Chen et al., 1995). Three species of large, irregular echinoids and a diversity of mollusks are abundant in a variety of habitats and all the abundant species are heterotrophic.

Because Tarawa lies in the equatorial upwelling region, the concentration of inorganic nutrients, phytoplankton biomass, and productivity is considerably elevated above that of atolls located in the subtropical gyres (Kimmerer and Walsh, 1981). This enhanced planktonic, and probably also benthic, primary production must be largely responsible for the abundance of macrobenthos. Although planktonic secondary production has been estimated to be of insufficient magnitude to directly support the fishery yield of the atoll (Kimmerer, 1995), only an estimated 8-10% of the planktonic primary production is consumed by zooplankton (W. Kimmerer, pers. comm.). This percentage leaves open the possibility that much of the benthos is supported by planktonic primary production. The abundance of suspension and deposit feeders in the benthos is consistent with this hypothesis. Bonefish, as well as many other fish species, rely largely on suspension and deposit feeding invertebrates for their food (personal observation), and therefore could be supported in large part indirectly by planktonic primary production.

Suspension and deposit feeders dominate the macrobenthos. The deep lagoon bottom is dominated by three deposit-feeding echinoids, a suspension-feeding gastropod (*Turritella cingulifera*), a deposit-feeding bivalve (unidentified tellinid), and a variety of suspension- and deposit-feeding polychaetes. The spectacular abundance of irregular echinoids indicates the importance of the detrital food chain. The muddy sediments (indicative of limited horizontal transport) and the absence of macroalgae or photosymbiotic foraminiferans indicate that the deep lagoon bottom community may ultimately be supported largely by planktonic production, although the possible role of benthic microalgae remains to be evaluated.

The shallower lagoon slope is dominated by a similar assemblage of echinoids and polychaetes, and some large suspension-feeding (*Anadara*) and grazing (*Strombus luhuanus, S. erythrinus,* and *S. variabilis*) mollusks. The latter species feed on attached and free-living (*Grateloupia*) benthic algae. The sand-flat community is dominated by bivalves (93% of all individuals encountered), including suspension-feeding, deposit-feeding, and chemo-symbiotic taxa. On the sand flat and shoals, *Strombus* is also abundant.

Seagrasses are locally dominant producers in the benthos and seagrass beds support a greater abundance of shellfish than adjacent areas. Seagrasses are known to facilitate the production of macrobenthos in a variety of ways (see above). The enhancement of particulate food supplies by hydrodynamic baffling and by production of seagrass detritus

can be important (Peterson et al., 1984). The importance of benthic plant detritus as a food source for suspension and deposit feeders living under the plants has been demonstrated in temperate kelp beds (Duggins et al., 1989) and probably also applies to seagrass beds. The fact that the most productive *Anadara* beds lie within seagrass beds on the sand flat, or directly lagoonward of such beds on the lagoon slope, may indicate the importance of seagrass primary production for this community.

Both the seagrass beds and associated shellfish resources appear to have increased substantially since World War II, perhaps as a result of increased fertilization by sewage-derived nutrients. The width of seagrass beds has more than doubled off South Tarawa between 1943 and 1984. Since World War II, the population of South Tarawa has increased by 1,700%. Associated with this increase is a large increase in sewage-derived nutrients that enter the lagoon through each tidal cycle. Although sewage-derived nutrients were found by Kimmerer (1995) to be unimportant in the nutrient budget of the southern lagoon as a whole, these nutrients may have considerable influence over the intertidal sand flat that they traverse. This influence is demonstrated by the high bacterial contamination in shellfish taken from the sand flat but not from offshore lagoonal habitats (Danielson et al., 1995).

The effect of causeway construction on seagrass beds is unclear. A correlation seems to exist between the presence of extensive seagrass beds and the lack of passages: the largest seagrass beds lie off the longest islets. Many small seagrass beds, however, including all the seagrass beds in North Tarawa between Bonriki and Buariki, lie immediately on the lagoon side of the passages. Seagrass beds changed markedly, with some portions expanding and other portions contracting, off the Taborio-Ambo passage after causeway construction (based on aerial photographs taken before causeway construction [1943] and after [1968 and 1984]).

Whatever the cause, the observed expansion of seagrass beds was probably partly responsible for the apparent increase in shellfish resources during the past several decades. Older residents of Tarawa recall a considerable increase in the abundance of *Anadara*, and then *Strombus luhuanus*, and modest increases in the abundance of *Gafrarium pectinatum, Asaphis violascens* (*te koikoi*), and *Atactodea striata* (*te katura*) since World War II (Johannes, 1992).

In contrast, Johannes (1992) noted that the edible sipunculan (*te ibo*) has become scarce in South Tarawa within living memory, and most of the worms now are taken in North Tarawa. This worm is generally found on sand flats that lie on the lagoon side of passes between islets (Nabuaka Tekinano pers. comm.). Thus, its disappearance from South Tarawa may be the result of closing the passages with causeways.

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APPENDIX I
Site Coordinates

Sand flat transects: all traversing the South Tarawa sand flat (shore to edge of sand flat), perpendicular to shore. Coordinates for origin on shore:

TRANSECT	LAT	LONG
Temaiku	1°22.302'N	173°08.624'E (E-W orientation!)
Bikenibeu	1°21.876'N	173°07.154'E
Bangantebure	1°21.805'N	173°05.686'E
Abarao	1°21.739'N	173°05.218'E
Eita E	1°21.73'N	173°04.75'E
Eita W	1°21.50'N	173°04.25'E
Tangintebu	1°21.339'N	173°03.840'E
Ambo	1°21.350'N	173°02.693'E
Banraeaba	1°20.55'N	173°01.80'E
Antenon	1°20.15'N	173°01.05'E
Nanikai	1°19.872'N	172°59.680'E
Betio	1°21.227'N	172°56.150'E

Lagoon stations:

STATION	LAT	LONG	DEPTH
L3	1°22.839'N	172°56.075'E	11 m
L4	1°22.828'N	172°57.767'E	20 m
L5	1°22.817'N	172°59.465'E	11 m
L6	1°22.889'N	173°06.340'E	6 m
L7	1°22.857'N	173°01.206'E	12 m
L8	1°22.842'N	173°02.899'E	15 m
L9	1°22.781'N	173°04.510'E	12 m
L10	1°26.711'N	172°55.727'E	17 m
L11	1°26.708'N	172°57.322'E	15 m
L12	1°26.703'N	172°58.057'E	17 m
L13	1°26.703'N	173°00.544'E	17 m
L14	1°30.581'N	172°55.186'E	8 m
L15	1°30.462'N	172°56.747'E	17 m
L16	1°30.521'N	172°58.274'E	11 m

Lagoon slope transects: Traversing the South Tarawa lagoon slope, all oriented N-S irrespective of shore-line orientation, and extend from 0.05' N of the sand flat to 0.55' N of the sand flat:

TRANSECT	LAT-Beginning	LAT-Ends	LONG
1	1°19.906'N	1°20.413'N	172°59'E
2	1°20.074'N	1°20.562'N	173°00'E
3	1°20.556'N	1°21.064'N	173°01'E
4	1°21.228'N	1°21.728'N	173°02'E
5	1°21.597'N	1°22.051'N	173°03'E
6	1°21.79'N	1°22.29'N	173°04'E
7	1°22.063'N	1°22.510'N	173°05'E
8	1°22.189'N	1°22.689'N	173°06'E
9	1°22.066'N	1°22.566'N	173°07'E

APPENDIX II
I-Kiribati names of marine invertebrates

Invertebrates for which indigenous names were recorded and those mentioned in this paper are listed with their authorities below. Indigenous names that apply to a group of species are labeled generic and listed under the wider taxonomic category to which they are applied as well as under the species/genus within that category to which I heard the name applied. I-Kiribati names that appear to be utilized inconsistently or otherwise are deemed to need further confirmation, are noted with a '?'. A '?' preceding a scientific name implies that the identity of the organism was difficult to ascertain, generally because no specimens were seen and the name was based on a description. Such species included solely on the basis of informant's descriptions are marked with an '*'. Names specific to southern Kiribati are denoted with an 'S', those to northern Kiribati with a 'N'. The definite article "te" leads species names in I-Kiribati. Names are based on interviews with a small number of people on Tarawa from 1992 to 1994, and do not include compilations from the literature (Banner & Randall, 1952; Lobel, 1978). The latter two papers were disregarded because they include several erroneous names.

Species	I-Kiribati name
CNIDARIA	
Cubozoa	
?Carybdea alata Reynaud, 1830*	te baitari
Scyphozoa	
?Cassiopea sp.*	te tia
Anthozoa - Scleractinia	
Branching corals (including *Pocillopora, Acropora*)	te enga (generic)
Massive corals, at least *Porites*	te atitaai (generic)
Mushroom corals (Fungiidae)	?te wenei (generic)
MOLLUSCA	
Bivalvia	

Mytilidae	
Modiolus auriculatus Krauss, 1848	
Arcidae	
Barbatia foliata (Forsskål, 1775)	?te nikarinei
Anadara uropigimelana (Bory de St Vincent, 1824)	te bun
Spondylidae	
Spondylus squamosus Schreibers, 1793	te koikoi n anti
Pteriidae	
Pinctada margaritifera (Linné, 1758)	te baeao
Pinnidae	te bwere, te katati (generic)
Atrina vexillum (Born, 1778)	te bwere, te katati (generic)
Pinna sp.	te bwere, te katati (generic)
Lucinidae	
Wallucina haddoni (Melvill & Standen, 1899)	
Codakia bella (Conrad, 1837)	te kairebwe, ?te nikarewerewe
Cardiidae	
Vasticardium angulatum (Lamarck, 1819)	te koikoi n tari
Acrosterigma unicolor (Sowerby, 1834)	incorrectly called te koikoi n tari by some
Fragum sueziense (Issel, 1869)	
Tridacna maxima (Röding, 1798)	te were
Tridacna squamosa Lamarck, 1819	te were matai
Tridacna gigas (Linné, 1758)	te kima
Hippopus hippopus (Linné, 1758)	te neitoro
Mesodesmatidae	
Atactodea striata (Gmelin, 1791)	te katura
Tellinidae	
Tellina (Quidnipagus) palatam (Iredale, 1929)	te nikatona
Tellina (Tellinella) crucigera Lamarck, 1818	?te kabwere
Tellina (Tellinella) virgata Linné, 1758	?te kabwere
Scissulina dispar (Conrad, 1837)	
Psammobiidae	
Asaphis violascens (Forsskål, 1775)	te koikoi[1]
Veneridae	
Gafrarium pectinatum (Linné, 1758)	te koumara
Dosinia amphidesmoides (Reeve, 1850)	
Pitar prora (Conrad, 1837)	
Timoclea marica (Linné, 1758)	te koumai
Gastropoda	
Trochidae	
?Tectus pyramis (Born, 1778)*	te baraitoa
Skeneidae	
Cyclostremiscus cingulifera (A. Adams, 1850)	
Turbinidae	
Turbo spp.	te matanin (generic)
Neritidae	

Nerita spp.	te kaban (generic)
Cerithiidae	
Rhinoclavis aspera (Linné, 1758)	
Turritellidae	
Turritella cingulifera Sowerby, 1825	
Naticidae	te tumara (generic)
Mammilla melanostoma (Gmelin, 1791)	te tumara (generic)
Polinices mammilla (Linné, 1758)	te tumara (generic)
Tectonatica robillardi (Sowerby)	
Strombidae	
Strombus erythrinus Dillwyn, 1817	
Strombus luhuanus Linné, 1758	te nouo
Strombus variabilis Swainson, 1820	te newenewe
Cypraeidae	te buro (small), (generic)
	te bure (large) (generic)
	te kabaau (some spp.) (generic)
Ranellidae	
Charonia tritonis (Linné, 1758)	?te buu, ?te tau
Cymatium muricinum (Röding, 1798)	te nimakaka, te wiiaau
Cassidae	
Cypraecassis rufa (Linné, 1758)	?te buu, ?te tau
Olividae	
Oliva miniacea (Röding, 1798)	te burebangaki
Terebridae	
Terebra spp.	te buki kakang (generic)
Elobiidae	
Melampus castaneus (Mühlfeldt, 1818)	te ningo ningo (generic)
Melampus flavus (Gmelin, 1791)	te ningo ningo (generic)
Opisthobranchia	
?Dolabella auricularia (Lightfoot, 1786)	te ingke (from "ink") not seen
Unidentified slug*	te ubaraniti
Unidentified slug*	te non
Cephalopoda	
Octopus sp. large*	te kika
Octopus sp. small*	te kikao
Octopus sp.*	te kaonako
Octopus sp.*	te riburibunimainuku
?Sepioteuthis lessoniana Lesson, 1830*	te riro
ECHINODERMATA	
Holothuroidea	
Holothuriidae	
Bohadschia vitiensis (Semper, 1868)	te kereboki (generic)
Holothuria atra Jaeger, 1833	te n tabanebane (specific)
"	?te nautong (S, specific)
Synaptidae*	te robwe (from 'rope')
Echinoidea	

?Diadematidae	te batinou
Laganidae	
Laganum depressum tonganense Agassiz, 1841	
Spatangidae	
Maretia planulata (Lamarck, 1816)	te katuiaia
Brissidae	
Metalia sternalis (Lamarck, 1816)	te takataka
Ophiuroidea	te kiko n ang (generic)
Asteroidea	
Acanthasteridae	
Acanthaster planci (Linné, 1758)*	te aa (?generic)
ARTHROPODA	
Crustacea	
land crab names from Makin Atoll*	te mama, te bukiroro, te batinana
other crab names*	te n tababa, te kaveana
Palinuridae	te nnewe (generic)
?Panulirus penicillatus (Olivier, 1791)*[2]	te nnewe, te urataake
?Panulirus versicolor (Latreille, 1804)*[2]	te kouratake
Scyllaridae	
?Parribacus sp(p).*	te mnau, te n tabataba
Coenobitidae	
Birgus latro (Linné, 1776)	te ai
Calappidae	
Calappa sp.	te nnon nnon
Carpiliidae	
Carpilius maculatus (Linné, 1758)	te tabanou
Grapsidae	
?Grapsus tenuicrustatus (Herbst, 1783)*	te kamakama
Gecarcinidae[3]	te manaimeri, te manai, te meri
Stomatopoda - Lysiosquillidae	
Lysiosquilla maculata (Fabricius, 1793)	te varo
SIPUNCULA	
?Sipunculus indicus	te ibo
larger sp.*	te ibo raro
ANNELIDA/Polychaeta	
?Amphinomidae*	te karau
HEMICHORDATA	
Ptychodera flava Eschscholtz	te bonubonu
Glossobalanus ?elongatus Spengel, 1904	te bonubonu

NOTES:

[1] The name te koikoi appears to traditionally pertain only to *Asaphis violascens*. However, people not well versed in traditional knowledge apply this name indiscriminately to a variety of bivalve species.

[2] Kouratake and urataake likely represent the same name, with koura and ura being variants of the polynesian "koura" for lobster, and either take or taake being a mispelling of the other.

[3] Tarawa has one or more species of *Cardisoma* as well as *Gecarcoida lalandi*; it is unclear if the indigenous name is specific to one of these or generic.

NOTE OF INSTRUCTIONS THAT WENT WITH MS:
Location of graphs and data in files (on disk): Files .wq1 in QPro for DOS, .wb1 in QPro for Windows. To find data for graphs, look under "series" for graph.

Figure	**File**	**Graph**
Fig. 1	none.....	
Fig. 2A	stransec.wq1	diversity #
Fig. 2B	stransec.wq1	toal by quadrat
Fig. 3	stransec.wq1	density 2
" (more)	"	densit across
Fig. 4	stransec.wq1	sum / m2
Fig. 5	stransec.wq1	te bun by site
Fig. 6	stransec.wq1	nouo transect
Fig. 7	stransec.wq1	koumara transec
Fig. 8	zoanthid.wb1	zo-zonation
Fig. 9	slopesum.wb1	zonation all
Fig. 10	slope-q.wb1	zonation across
Fig. 11	slope-q.wb1	bun in bed
Fig. 12	bunslope.wq1	bun size
Fig. 13	bunslope.wq1	bun tr 4,6,7
Fig. 14	none.....	
Fig. 15	lansum1.wq1	catch per perso
Fig. 16	lansum1.wq1	total catch

Figure 1 is map of Tarawa with major habitats outlined, thus it is the same base map as was requested for our reef ms (also Figure 1 there). In addition, please mark the location of seagrass beds (see sketch) and two sets of transects on this same map, as follows:

Set 1: traversing the S Tarawa sand flat (shore to edge of sand flat), perpendicular to shore. Please print name of each transect (based on locality name), at each location (coordinates given for origin on shore; see sketch for rough location):

TRANSECT	LAT	LONG
Temaiku	$1^{O}22.302$	$173^{O}08.624$ (note E-W orientation!)
Bikenibeu	$1^{O}21.876$	$173^{O}07.154$
Bangantebure	$1^{O}21.805$	$173^{O}05.686$
Abarao	$1^{O}21.739$	$173^{O}05.218$
Eita E	$1^{O}21.73$	$173^{O}04.75$
Eita W	$1^{O}21.50$	$173^{O}04.25$
Tangintebu	$1^{O}21.339$	$173^{O}03.840$
Ambo	$1^{O}21.350$	$173^{O}02.693$
Banraeaba	$1^{O}20.55$	$173^{O}01.80$
Antenon	$1^{O}20.15$	$173^{O}01.05$
Nanikai	$1^{O}19.872$	$172^{O}59.680$
Betio	$1^{O}21.227$	$172^{O}56.150$

Set 2: traversing the S Tarawa lagoon slopes, these transects are oriented N-S, irrespective of shore-line orientation, and extend from 0.05' N of the sand flat to 0.55' N of the sand flat at the following longitudes. Please draw in transect line and label with transect number.

TRANSECT	LONG	LAT-Beginning	LAT-Ends
1	172°59'	1°19.906'	1°20.413'
2	173°00'	1°20.074'	1°20.562'
3	173°01'	1°20.556'	1°21.064'
4	173°02'	1°21.228'	1°21.728'
5	173°03'	1°21.597'	1°22.051'
6	173°04'	1°21.79'	1°22.29'
7	173°05'	1°22.063'	1°22.510'
8	173°06'	1°22.189'	1°22.689'
9	173°07'	1°22.066'	1°22.566'

Figure 14 is another map of Tarawa, copied from Richmond (1990: Fig. 3). Please scan and indicate major sediment types by different shading as they appear on map (a clean copy is enclosed. Then please map the following 14 lagoon bottom stations on this map (below). Finally, please draw in via three lines, the distributional limits of the 3 echinoid species, as shown on sketch.

Lagoon stations:

L3: 1°22.839'N, 172°56.075'E
L4: 1°22.828'N, 172°57.767'E
L5: 1°22.817'N, 172°59.465'E
L6: 1°22.889'N, 173°06.340'E
L7: 1°22.857'N, 173°01.206'E
L8: 1°22.842'N, 173°02.899'E
L9: 1°22.781'N, 173°04.510'E
L10: 1°26.711'N, 172°55.727'E
L11: 1°26.708'N, 172°57.322'E
L12: 1°26.703'N, 172°58.057'E
L13: 1°26.703'N, 173°00.544'E
L14: 1°30.581'N, 172°55.186'E

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ATOLL RESEARCH BULLETIN

NO. 488

VARIABLE RECRUITMENT AND CHANGING ENVIRONMENTS CREATE A FLUCTUATING RESOURCE: THE BIOLOGY OF *ANADARA UROPIGIMELANA* (BIVALVIA: ARCIDAE) ON TARAWA ATOLL

BY

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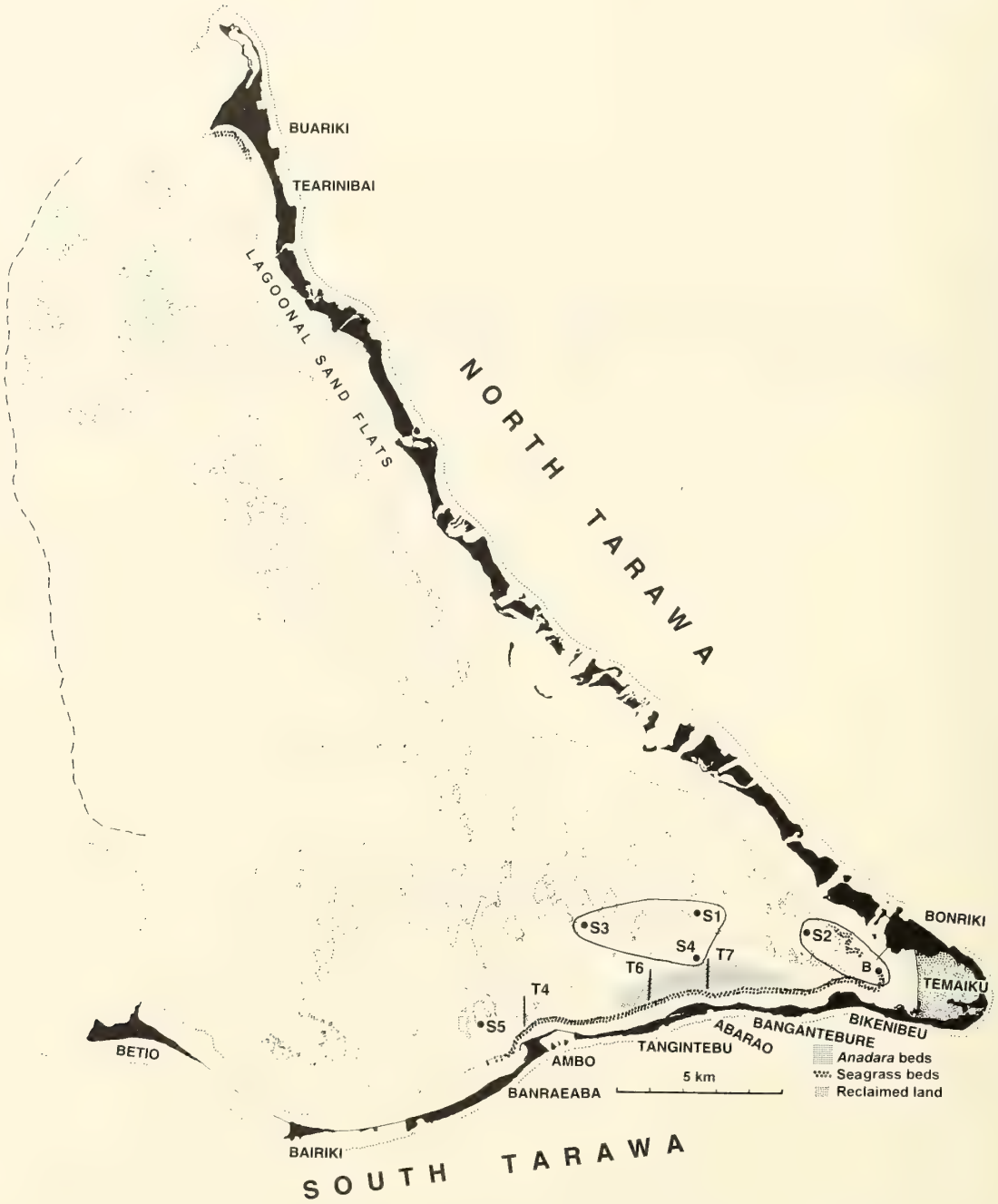

Figure 1. Map of Tarawa showing location of lagoon slope *Anadara* bed, major seagrass beds (including B = Bonriki seagrass bed), five shoals sampled (S1 – S5), and lagoon slope transects (T4, 6, 7) mentioned in text. The centers of the two most recent recruitment events are encircled. These are the areas that were dominated (>50% of individuals / sample) by the 10-20 mm and 20-30 mm-size classes.

VARIABLE RECRUITMENT AND CHANGING ENVIRONMENTS CREATE A FLUCTUATING RESOURCE: THE BIOLOGY OF *ANADARA UROPIGIMELANA* (BIVALVIA: ARCIDAE) ON TARAWA ATOLL

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ABSTRACT

The arcid bivalve *Anadara uropigimelana* (*te bun*) is the most important shellfish resource in the central atolls of Tungaru (former Gilbert Islands), with a yearly catch of ca. 1400 tons on South Tarawa alone. Species of *Anadara s.s.* are also important in artisanal shellfisheries on several central Pacific islands. Tungaru atolls lying in the highly productive zone of equatorial upwelling harbor dense *te bun* beds, while those occurring outside this zone have fewer *Anadara*. *Te bun* are abundant in seagrass beds, lagoonal shoals, and shallow-lagoon bottoms. They reproduce year round with a lunar spawning periodicity. Size frequency data and observations on the occurrence of small juveniles indicate that, despite frequent reproduction, there is high spatio-temporal variation in recruitment within the Tarawa lagoon. One massive recruitment event in 1993 opened a novel fishery in Bonriki village, where no *te bun* were available for two decades previously. Highly variable recruitment, as well as changes in the extent of seagrass habitats, may explain marked historical fluctuations in the abundance of this important resource.

INTRODUCTION

Human populations on atolls, more than on any other type of island, have traditionally relied on the ocean for much of their nourishment. Although a great diversity of marine species is exploited, fishes constitute the most important resource. Molluscs are widely exploited on atolls, but perhaps nowhere as heavily as on the equatorial atolls of the Tungaru (former Gilbert) Islands in the Republic of Kiribati.

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These atolls lie in the equatorial upwelling zone, and the high productivity of the region influences many aspects of their form and biota (Paulay, 1997). Tarawa is typical of these atolls in its productivity but unusual in that, as the metropolitan center of Kiribati, it has the largest human population of any atoll in the Pacific. One manifestation of the high productivity is the large populations of several bivalve and gastropod species on lagoonal sand flats, slopes, and shoals (Paulay, 2001). Much of the population on Tarawa still relies on the ocean for their protein need and the abundant molluscan resources of the atoll are heavily exploited.

Tarawa is a triangular atoll with islet-studded eastern and southern rims and a submerged western flank (Fig. 1). Much of the human population lives along the southern rim ("South Tarawa"), where islets have been connected entirely by causeways. In contrast, North Tarawa remains rural and has considerably lower population density. The lagoon has striking physical, chemical, and biological gradients north-to-south and west-to-east, as a result of the largely unidirectional flushing of the lagoon across the submerged western barrier reef. The largest shellfish populations are found near the southeastern lagoon where they occur on the intertidal sand flats lying lagoonward of the islands, on the numerous shoals that dot the lagoon, as well as on the shallower parts of the lagoon bottom (Paulay, 2001).

The arcid bivalve *Anadara uropigimelana* is the most important shellfish resource on Tarawa, as well as throughout central Kiribati. Its importance stems in part from its abundance, large size and accessibility. It is the largest (to 7+cm) of the commonly harvested shellfish species (giant clams are now a rare resource in the area) and also one of the most common; the largest *Anadara* bed in South Tarawa has a mean population density of 14 m^{-2} clams. In South Tarawa alone, ca. 1400 tons of *te bun* are harvested annually. Mean daily *Anadara* catches average 9 kg each for several hundred subsistence gatherers that collect daily on the sand flat and 112 kg each for the ca. 35 commercial divers working from canoes on an offshore bed (Paulay, 2001). No other island group in Polynesia and Micronesia supports similarly extensive molluscan fisheries. Even among the large and productive islands of Melanesia, molluscan fisheries are less significant. Thus Squires et al. (1973) found that near Suva, Fiji, where *Anadara* is the most important marine shellfish harvested, the average daily catch of gatherers was 2 kg. Being abundant in near-shore seagrass beds accessible by wading, as well as in deeper beds requiring canoes and diving gear, *te bun* are accessible to all members of the population. Consequently, most households partake in shellfish gathering (Phillips, 1995).

Reflecting the importance of this shellfish is the significant role it plays in traditional Kiribati society. On Abemama, if fish are not available, *te bun* are presented at traditional gatherings in a meeting house (*maneaba*). *Te bun* shells are worn around the waist on dancing costumes by women and girls. *Anadara* shells are still in use, especially by older men and women for grating mature coconut meat and babai (giant swamp taro, *Cyrtosperma chamissonis* (Schott) Merrill).

Here we summarize what is known about the biology of *Anadara uropigimelana* on Tarawa, considering its identity, distribution, ecology, reproductive biology, and population dynamics.

METHODS

The size structure of *Anadara* in several areas was surveyed during a general benthic lagoon survey, as outlined in Paulay (2001). In addition to samples obtained in that survey, we sampled five shoals in the southeastern lagoon of Tarawa Atoll (Fig. 1). At these shoals, ten 0.25 m^2 quadrats were haphazardly tossed on the top of the shoal and all *Anadara* encountered within counted and measured. When fewer than 100 *Anadara* were so encountered, additional areas in the same area were systematically searched until at least 100 clams were found. All clams were measured with dial calipers to the nearest mm. Shellfish gatherers were surveyed as described in Paulay (2001).

The present distribution and qualitative abundance of *Anadara* was evaluated on several atolls from site visits by Tebano. Historical changes in the abundance of the species were recorded from the recollection of older informants on Abemama, Maiana, and Abaiang Atolls.

RESULTS AND DISCUSSION

Identity of *te bun*

Identification of species of *Anadara* is difficult at present, because the genus includes numerous closely related forms whose phenotypic variability and nomenclatural identity have not been fully worked out. As a result, identifications of Indo-West Pacific *Anadara* species in the nontaxonomic literature are often unreliable.

While several *Anadara* species occur in the western Pacific (e.g. at least six species in Fiji; Paulay, pers. obs.), only two, *A. antiquata* (Linné, 1758) and *A. uropigimelana* (Bory de St Vincent, 1824), are known from islands of the Pacific tectonic plate (Paulay, 1996). They both belong to *Anadara s.s.*, are illustrated by Kilburn (1983), and although they exhibit considerable intraspecific variation, can be readily distinguished as follows (Fig. 2):

1. The ribs of *A. antiquata* become gradually grooved with age, starting with a single central groove and often followed by the development of smaller grooves on either side. This grooving is best developed on the anterior half of the shell and makes it appear as if the ribs were bifurcating (which, however, they are not). The ribs (as well as the interstices) of *A. uropigimelana* are finely grooved by several, inconspicuous, minute grooves that do not increase in number as the animal grows.
2. The periostracum of *A. antiquata* is coarsely bristled with large, flattened setae arising from the interstices as well as from the grooves that develop on the ribs as the animal grows. In contrast, the periostracum of *A. uropigimelana* is velvety, with series of minute bristles arising from the numerous fine grooves on both ribs and interstices.

3. The shell of *A. antiquata* is less inflated, more posteriorly produced (umbo lying relatively more anteriorly), and has the posterior slope gently demarcated. In contrast, the posterior slope of *A. uropigimelana* is offset by a strong break in slope from the rest of the shell.
4. *Anadara antiquata* has 35-39 ribs among the samples we examined compared with 31-35 in *A. uropigimelana*.

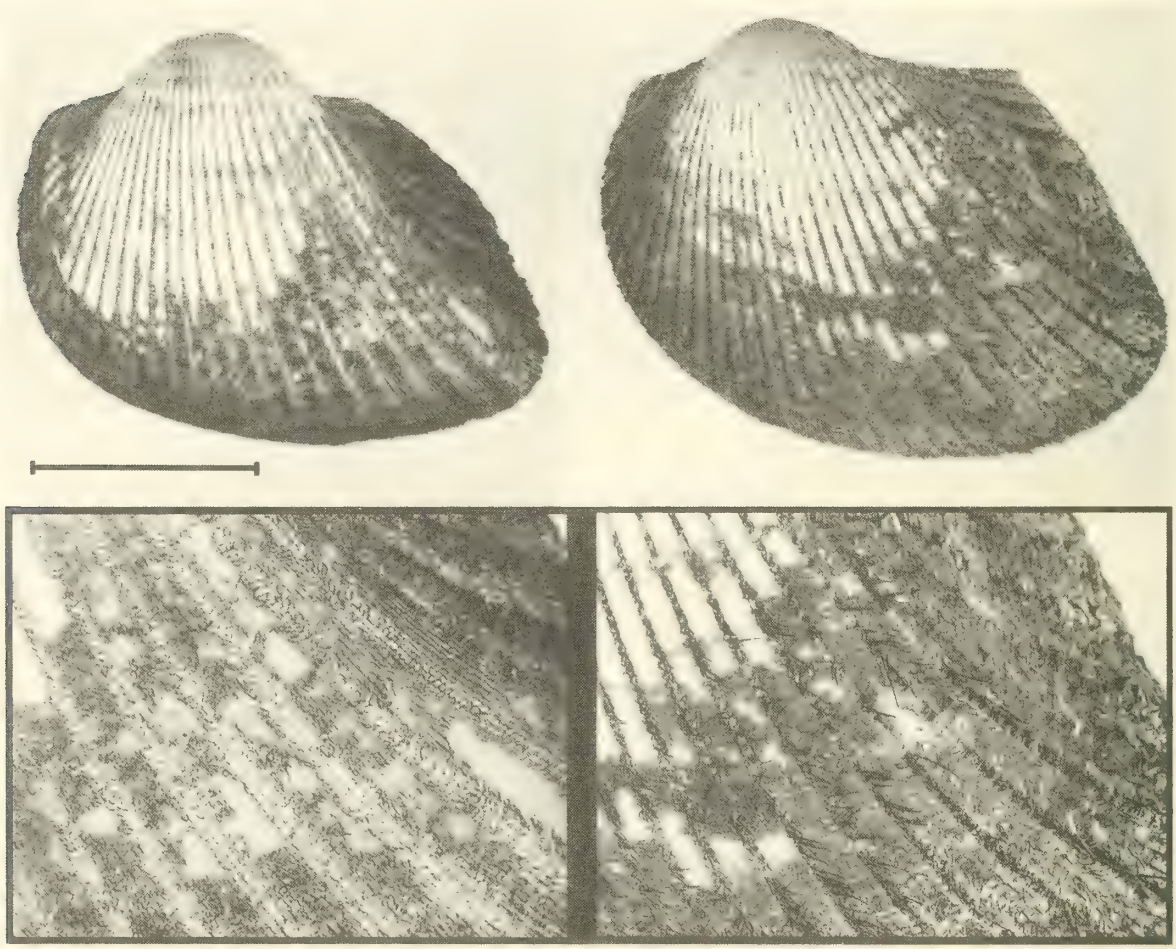

Figure 2. *Anadara uropigimelana* (left, Tarawa, UF 282607; Tarawa) and *Anadara antiquata* (right, UF 282606, Tonga). Scalebar: 2 cm.

Both *Anadara antiquata* and *Anadara uropigimelana* are widely distributed from East Africa to the Central Pacific. The occurrence of both species appears to be patchy in Oceania (Paulay, 1996). *Anadara antiquata* is known in Oceania from the Mariana Islands (Guam, Saipan), Tonga (Tongatapu), Cook Islands (Aitutaki, ?Holocene fossil), and Hawaii (Oahu, Pleistocene fossil). *Anadara uropigimelana* is known from the Federated States of Micronesia (Chuuk), and the Marshall, Tungaru, Tonga (Tongatapu and Haapai), and Society (Tahiti) Islands (Paulay, 1996 and pers. obs.). This patchy distribution is likely attributable in part to the relatively recent colonization of the Central Pacific by *Anadara*. Both species are restricted to lagoonal habitats in Oceania, and all lagoons are stranded in this area during glacial low sea stands (Paulay, 1990; 1996).

Thus the present occurrence of these species in the region must postdate the Holocene sea-level rise, unless they survived in unexpected refugia.

The patchy distribution of *Anadara* species likely is also related to the patchy distribution of their preferred habitats. Both species have a tendency to be associated with marine angiosperms: *Anadara antiquata* with mangroves; and *A. uropigimelana* with seagrass beds. On Guam, *A. antiquata* is restricted to muddy sands adjacent to mangroves and is also very common in such habitats in Fiji. *Anadara uropigimelana* appears to be absent near mangrove habitats, but is common in seagrass beds. We have collected this species in seagrass beds in Kiribati, Tonga, and the Marshall Islands. Although *A. uropigimelana* does occur outside of seagrass beds, including deeper lagoonal habitats (Paulay, 2001), its abundance in seagrass meadows is generally higher than in adjacent sand-flat habitats (Tebano, 1990).

These two species of *Anadara*, which form the basis of local fisheries on many Pacific islands where they occur, including New Caledonia (Baron and Clavier, 1992), Fiji (Squires et al., 1973), Tonga (Spennemann, 1987), Chuuk (Federated States of Micronesia, A. Davis, pers. comm.), and prehistorically in the Mariana Islands (Amesbury, 1999; see below) as well as in Kiribati (Tebano, 1990), although they are recorded in the literature under a variety of names.

Abundance within Kiribati

Anadara uropigimelana is widely distributed in the Tungaru Islands of Kiribati, but shows marked differences in abundance among atolls. It is uncommon on the northernmost atoll of Butaritari, abundant on all the north-central atolls (Marakei, Abaiang, Tarawa, Maiana and Abemama), rare on Nonouti, and unknown on other southern atolls, although it may occur there in low population densities (Table 1). The species is also rare on Majuro Atoll of the neighboring Marshall Islands just to the north. Although other atolls in the Marshalls were not searched for *Anadara*, the lack of a local fishery and importation of *te bun* from Kiribati suggests that they are generally rare there. Attempts to establish shell beds by transplanting *Anadara* to atolls in southern Kiribati (Tabiteuea North in 1981 and 1984; Onotoa in 1984), although not recently evaluated, appear to have failed. Bolton (1981), in one of her evaluations of Tabiteuea Atoll for *te bun* transplant, noted the general scarcity of shellfish there and speculated that this may be due to unfavorable environmental conditions.

The location of the belt of atolls with dense *Anadara* corresponds to the zone of equatorial upwelling, both centered at 0-3°N latitude. This correlation strongly suggests that large *Anadara* beds develop only where abundant food supplies are available, as a result of high planktonic productivity resulting from upwelling-derived nutrient enrichment (Kimmerer and Walsh, 1981; Kimmerer, 1995).

Ecology

Anadara is most common on Tarawa in: 1) seagrass beds of the lagoonal sand flat; 2) a large shell bed on the lagoon slope at 1-8 m depths in the southeastern lagoon; and 3) several shallow (0-2 m) sandy shoals in the southeastern lagoon (Fig. 1).

Occasional *Anadara* are also encountered on deeper lagoon bottoms; however, these likely represent stragglers and appear not to constitute a significant resource. Abundance data and stock estimates of this and other shellfish on the sand flat and lagoon slope are presented in Paulay (2001).

Table 1 Abundance of *Anadara* from Majuro to South Tungaru

Atoll	***Anadara* abundance**	**Latitude**
Majuro	+	7°10'N
Butaritari	++	3°10'N
Marakei	+++	2°00'N
Abaiang	+++	1°50'N
Tarawa	+++	1°30'N
Maiana	+++	1°00'N
Abemama	+++	0°20'N
Aranuka	?	0°10'N
Nonouti	++	0°40'S
N Tabiteuea	-/+	1°10'S
Beru	?	1°20'S
S Tabiteuea	-/+	1°30'S
Onotoa	-/+	1°50'S

All islands in Tungaru except Makin, Kuria, Nikunau, Tamana, and Arorae (which all lack functional lagoons and thus appropriate habitats for *Anadara*) are listed together with Majuro of the neighboring Marshall Islands. Abundance is depicted as absent or very rare (-/+), rare (+), occasional (++), abundant (+++), or unknown (?).

Unlike some anadarine bivalves (e.g. *Anadara granosa* - Broom, 1985), *Anadara uropigimelana* remains byssate throughout life. All juveniles <15 mm in size we encountered were attached to rubble or adult shells (Fig. 3; see below). This habit likely limits the distribution of *Anadara* to sediments with a rubble component such as coral gravel or shell hash. All the large *te bun* beds on Tarawa occur in gravely sand. Similarly, the two best *te bun* beds on Maiana Atoll are uniquely characterized by the presence of both hard and soft substrata (Tebano, 1990).

Although humans are undoubtedly the most important predator on *te bun* today, removing much of the production of this species from South Tarawan waters (Paulay, 2001), several marine predators also take their toll. The presence of numerous freshly crunched *te bun* shells, especially on shoals, appears to be evidence of ray predation. Rays were commonly seen in the southeastern lagoon and were the only species observed in the lagoon that is known to produce such damage. *Anadara* of all sizes were seen crushed, as were shells of the much larger (up to 13+ cm) bivalve *Periglypta sowerbyi* (Deshayes, 1853). *Te bun* clearly do not have a size refuge from these predators.

Large piles of *Anadara* shells frequently are found adjacent to patch reefs along the outer margin of the sand flat and lagoon slope. Most of these shells are intact or have

only small nicks taken out of them. No potential predators that could be responsible for these piles were seen near these patch reefs. These piles may be the result of the activities of potentially night-active octopus or fish.

Bonefish (*Albula glossodonta* (Forsskål, 1775)) are probably the most abundant molluscivorous fish in the lagoon (Beets, 2001). A study of bonefish gut contents revealed that *te bun* were a minor component of their diet, with only 4 shells seen in 111 (91 with contents) stomachs surveyed. All *te bun*, as well as other bivalve shells in bonefish stomachs, were small (<30 mm), indicating that only juveniles are vulnerable to bonefish predation (Beets, 2001).

Several species of naticid gastropods and the ranellid gastropod *Cymatium muricinum* (Röding, 1798) are important predators on bivalves in Tarawa. Both appear to prefer other bivalves than *Anadara*, although the *C. muricinum* has been observed feeding on *te bun* (Yamaguchi et al., n.d.). Both occur in moderate abundance on sand flats and are taken by shellfish gatherers. These gastropods are fairly small relative to *Anadara*, and the clam attains a refuge in size from them.

Reproductive biology

Tebano (1990, pers. obs.) found that *Anadara* on Tarawa reproduces year-round, spawning monthly around the full moon. A similar cycle of year-round spawning and one two-month-long gametogenic cycles were reported for *A. antiquata* in the Philippines (Toral-Barza and Gomez, 1985). In contrast, Baron (1992) found that "*A. scapha* (Linné)" (the identity of this species is dubious as Linné did not describe an *A. scapha*; it may represent *A. uropigimelana*) spawns only during the southern summer in New Caledonia. This difference could be attributable to the greater seasonality of New Caledonia (ca. 21°S) and/or to potential interspecific differences.

Tebano (1990) showed that gonadal development is first seen in *te bun* of a length of 27 mm, and mature gonads are first found in females of 38 mm length and in males of 42 mm length. In southwest New Caledonia, *A. "scapha"* was found with developing gonads of a length of 22 mm and first spawned at 30 mm. While we found *te bun* to reach a size of at least 73 mm, the New Caledonian form reaches a predicted maximum size (based on a von Bertalanffy equation) of 52 mm (Baron, 1994).

Tebano (1990) found that while the overall sex ratio of *te bun* among all samples was near 1:1, significantly biased sex ratios, ranging between 0.4-2.1, were observed in individual samples. No evidence for simultaneous hermaphroditism was found, and the males and females showed completely overlapping size distributions. Tebano (1990) suggested that *te bun* may exhibit some type of sequential hermaphroditism. Baron (1992) similarly found no evidence for simultaneous hermaphrodites in *A. "scapha"* in New Caledonia, but observed a male-biased sex ratio of 1.47. He also showed that small size classes were significantly male dominated while large size classes were female dominated, and proposed that the species may be a protandric hermaphrodite. Toral-Borza and Gomez (1985) also showed minor departures toward a male-biased sex ratio in *A. antiquata* in the Philippines.

Little is known about the larval biology of *Anadara s.s.* Yamaguchi et al. (n.d.) found some arcid larvae in lagoonal plankton samples on Tarawa. The life span of *Anadara uropigimelana* veligers is not known, but likely exceeds the lagoonal residence time of about one week (Chen et al., 1995), as a considerable pelagic period would be necessary to colonize Kiribati, especially since colonization must have occurred within the past 8000 years (see below).

Population dynamics - recruitment

Although *te bun* appear to spawn monthly, recruitment is episodic, and sizable recruitment events are uncommon. Juveniles are usually rare but can be locally abundant at certain times, indicating high spatio-temporal variability in recruitment. The majority of sites we sampled were dominated by one or a few striking size classes, presumably reflecting one or a few major past recruitment events that were responsible for each clam bed. Size-frequency distribution of *Anadara* samples differed among different sites within the lagoon, indicating that recruitment events were localized.

The rarity of new recruits was noted by Yamaguchi et al. (n.d.), who was unable to find any in the field but obtained some on spat collectors made of coconut husk. Our initial attempts to find juveniles also failed. These attempts included a survey of the sand-flat molluscan fauna that included sieving sediment from 72, 0.25 m^{-2} quadrats in *Anadara* habitat, and visual searches of rubble in many areas on the sand flat and on shoals. Later we observed small (9 mm mean, range of 5-25 mm) *Anadara* occasionally attached to the posterior third of the shells of adults in the dense lagoon slope *Anadara* bed (Fig. 3). In three samples, the average adult had 0.15 ± 0.08 juveniles attached (N=223 adults; s.d. among three samples). Although we examined numerous other potential substrata (dead *Anadara* and other shells, reef rubble) in the area and searched through large areas of sand (see Paulay, 2001), all juveniles encountered in the lagoon slope bed were attached to living adults. These beds have an abundance of adults and little rubble. The smallest juveniles were attached near the posterior margin of adults, with progressively larger ones found further down toward mid shell. At around 20 mm, size, juveniles took up a free-living existence (Fig. 3).

In contrast to the general rarity of juveniles and to their close association with adults only in the lagoon-slope *te bun* bed, we found abundant juveniles attached to reef rubble at Shoal 2 in June 1993 (Fig. 4). Adult clams were uncommon at this location and hosted only a few juveniles. No quantitative measures of population density were made, but juveniles occurred at estimated densities of tens to hundreds m^{-2}. These juveniles appear to represent a large recruitment event in the area (see below).

One or a few size classes tend to dominate among *Anadara* at any given location (Fig. 4, Table 2). Dominant size classes appear to represent particularly successful, localized, recruitment events. For example, two size classes, 10-20 mm and 20-30 mm, were particularly abundant during June-August, 1993. The distribution of these attests to the geographically patchy nature of each recruitment event: the first dominated the southeastern corner of the lagoon (sites S2, B) and the second was abundant off of Tangintebu (S1, S3, S4) (Fig. 1). The first event was particularly striking because of the

great abundance of *te bun* it represented (see below). The growth rate of *Anadara* from this event was rapid, with clams nearly doubling in length between June, 1993 and February, 1994 (Fig. 5).

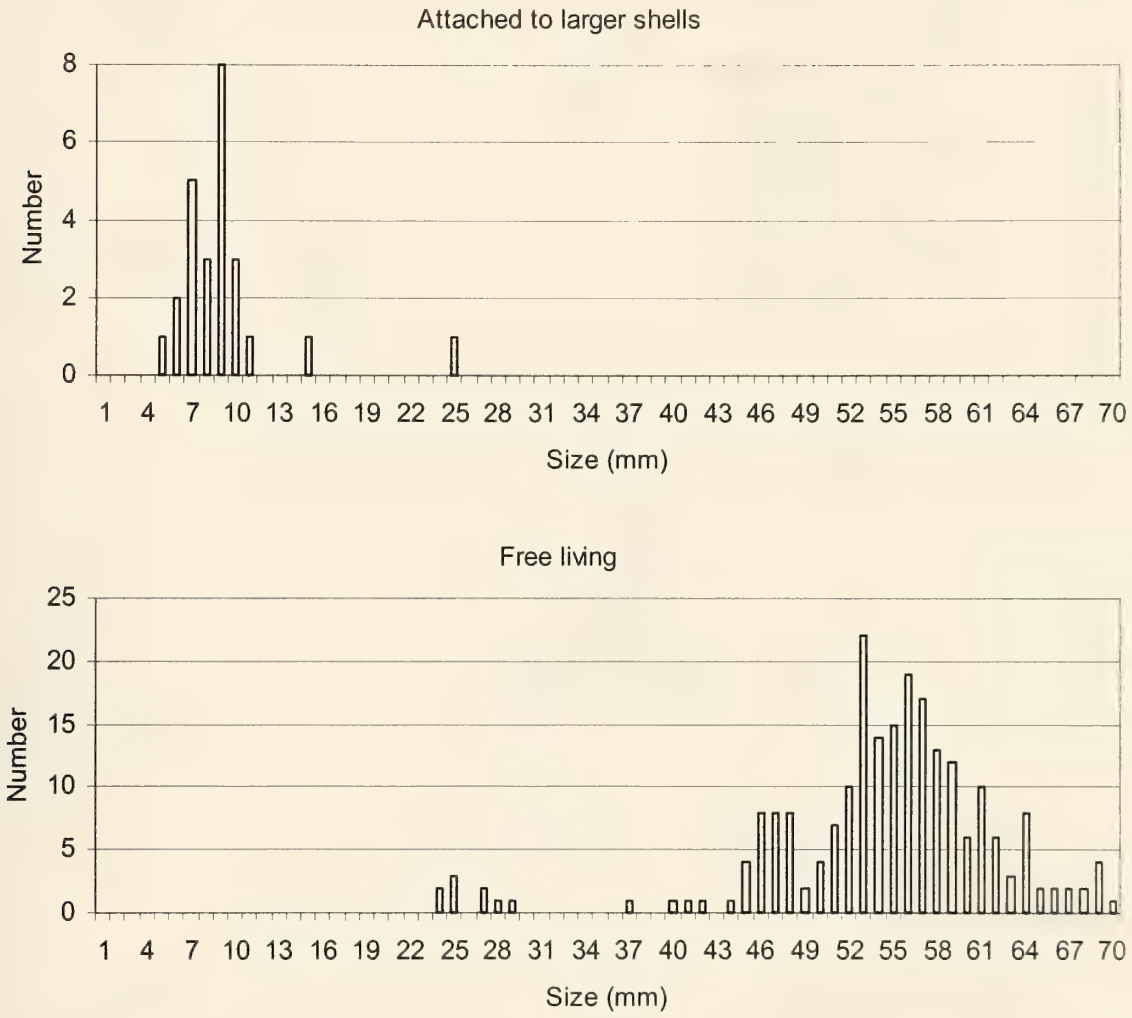

Figure 3. Size frequency distribution of free-living and attached (to larger conspecifics) *Anadara uropigimelana* in the Tangintebu-Bangantabure lagoon slope *te bun* bed (173°05.3'E; 1°22.2'N) in June 1993.

This recruitment event created a novel fishery in adjacent Bonriki. Until June 1993 the venerid clam *Gafrarium pectinatum* (Linné, 1758) was the main targeted species in the Bonriki-Temaiku area where, on the wide sand flat, it is particularly abundant (Paulay, 2001). *Anadara* did not occur in catches from this area at that time. Interviews with resident gatherers established that *te bun* were unknown in the Bonriki-Temaiku area during the past 20 years even though there is a well developed seagrass bed on the lagoonal margin of the sand flat that appeared to be reasonable *Anadara* habitat. By February 1994, when the new recruits increased to a harvestable size (Fig. 5), gathering activity shifted almost completely from *Gafrarium* to *Anadara*, a preferred food because of its larger size as well as its great abundance at the time. This shift also involved a move by gatherers from mid-sand flat *Gafrarium* habitat to the

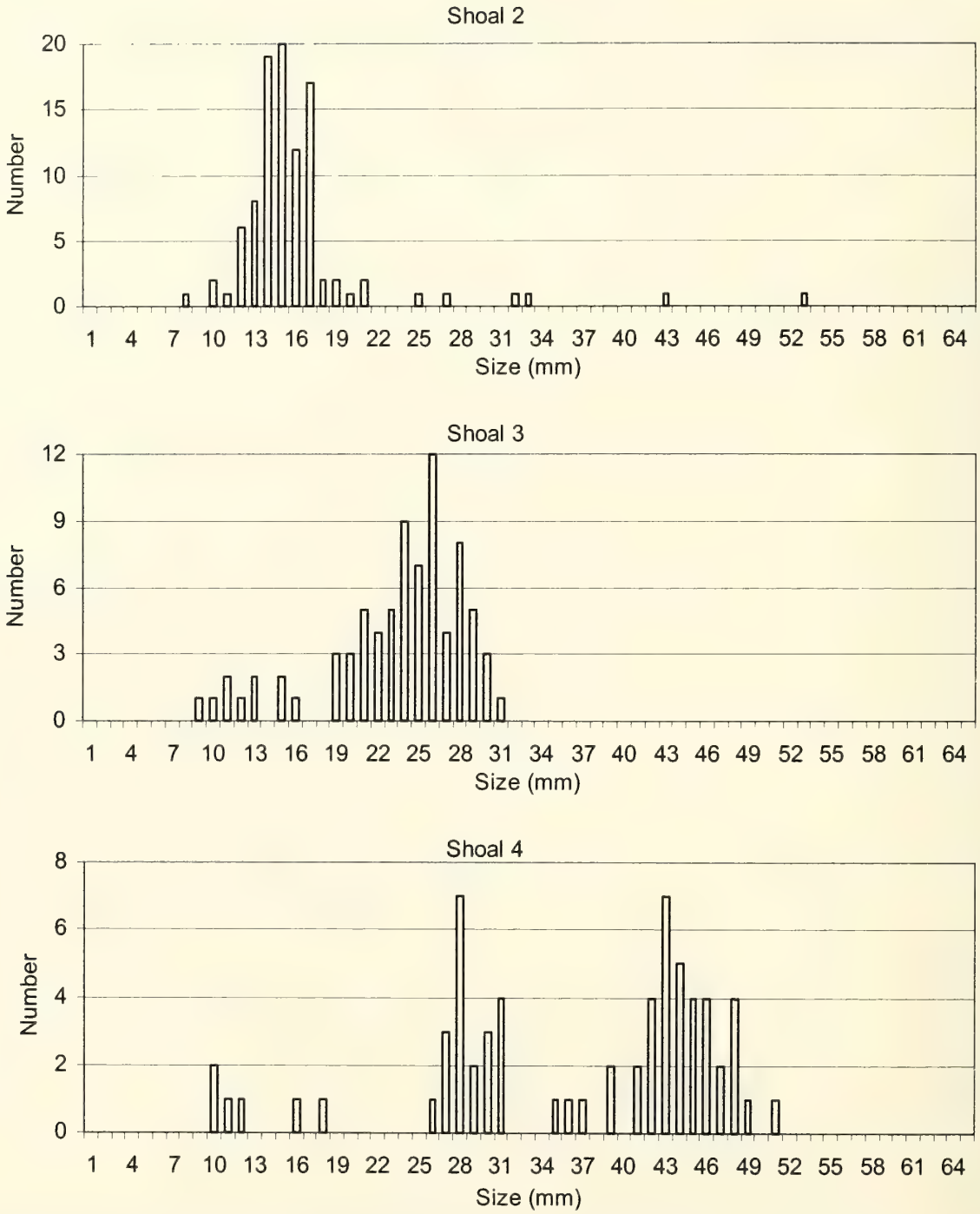

Figure 4. Examples of size frequency distribution of *Anadara* at different sites. Based on quadrat samples at shoals 2, 3, 4 (see Figure 1 for locations).

seagrass beds lying on the lagoonal edge of the sand flat adjacent to Bonriki village where the *Anadara* recruitment was localized (Fig. 1). Interviews established that this shift in harvesting focus took place in the second half of 1993. An average of 30-40 people harvested *Anadara* in the Bonriki bed during good low tides in February 1994 (data from gatherer study outlined by Paulay, 2001) with mean catch weight of 13 kg

compared to overall South Tarawa-wide mean shellfish catch weight of 8 kg (Paulay, 2001). The harvested *te bun* were 26+/-5 mm (N=100) (Fig. 6), in the same size range as on Shoal 2 (29+/-6 mm) at that time. In contrast, *te bun* caught at the same time west of Bikenibeu were considerably larger (44+/-8 mm; N=80) with <30 mm shells virtually absent (Fig. 6).

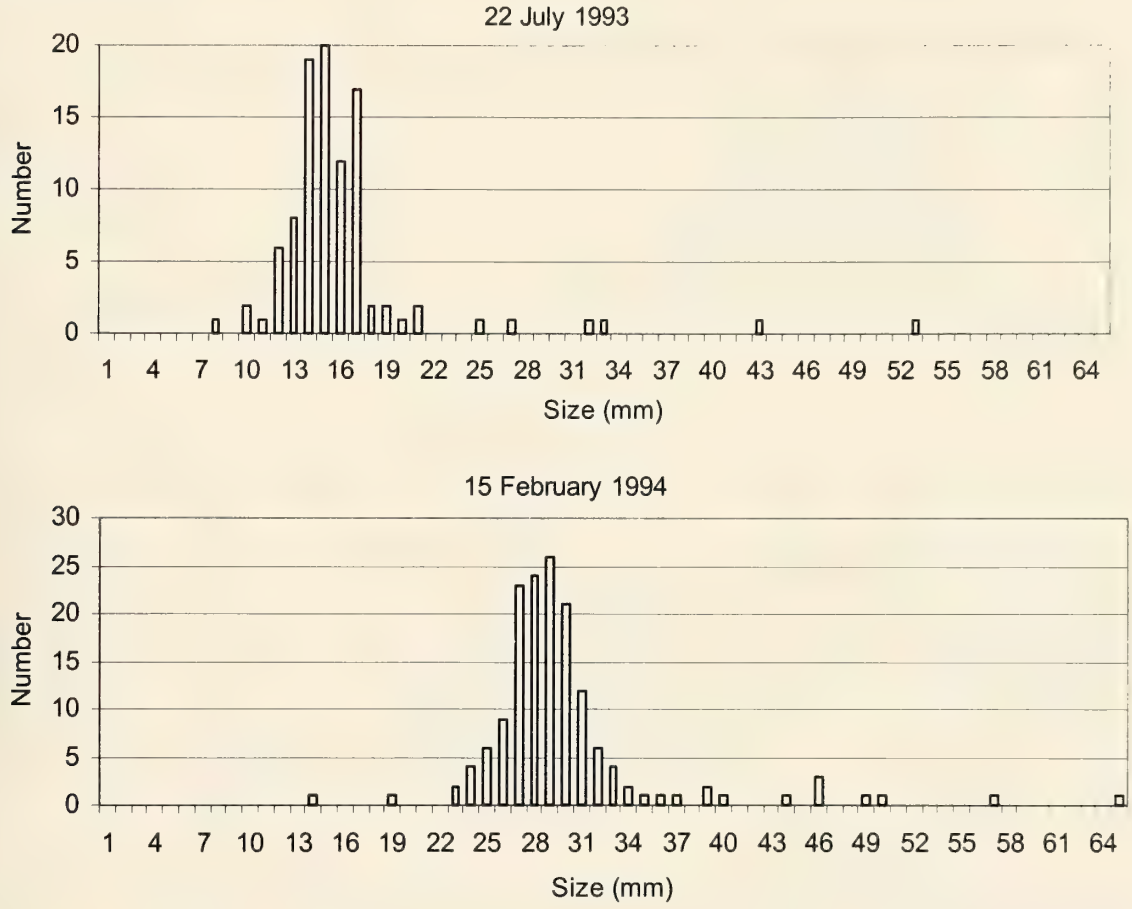

Figure 5. Growth of *Anadara* at Shoal 2 between 22 July 1993 and 15 February 1994.

Table 2 Dominant size classes of *Anadara* at different sites

Site	10-20mm	20-30mm	30-40mm	40-50mm	>50mm
S5	++	++	++	+	+
T4	+	+++	+	-	-
S3	+	+++	+	-	-
T6	+	+	++	+	++
S1	+	+++	-	-	-
S4	+	++	+	+++	+
T7	+	+	+	+	+++
S2	+++	+	+	+	+

Abundance data for major size classes at 9 sites, arranged east to west (Fig. 1). Size class recorded as absent (-), constituting 1-19% (+), 20-49% (++) or 50+% (+++) of individuals. Sites

with T numbers correspond to transects on lagoon slope (see Paulay, 2001); sites with S numbers correspond to shoals. All sampled in June-August 1993.

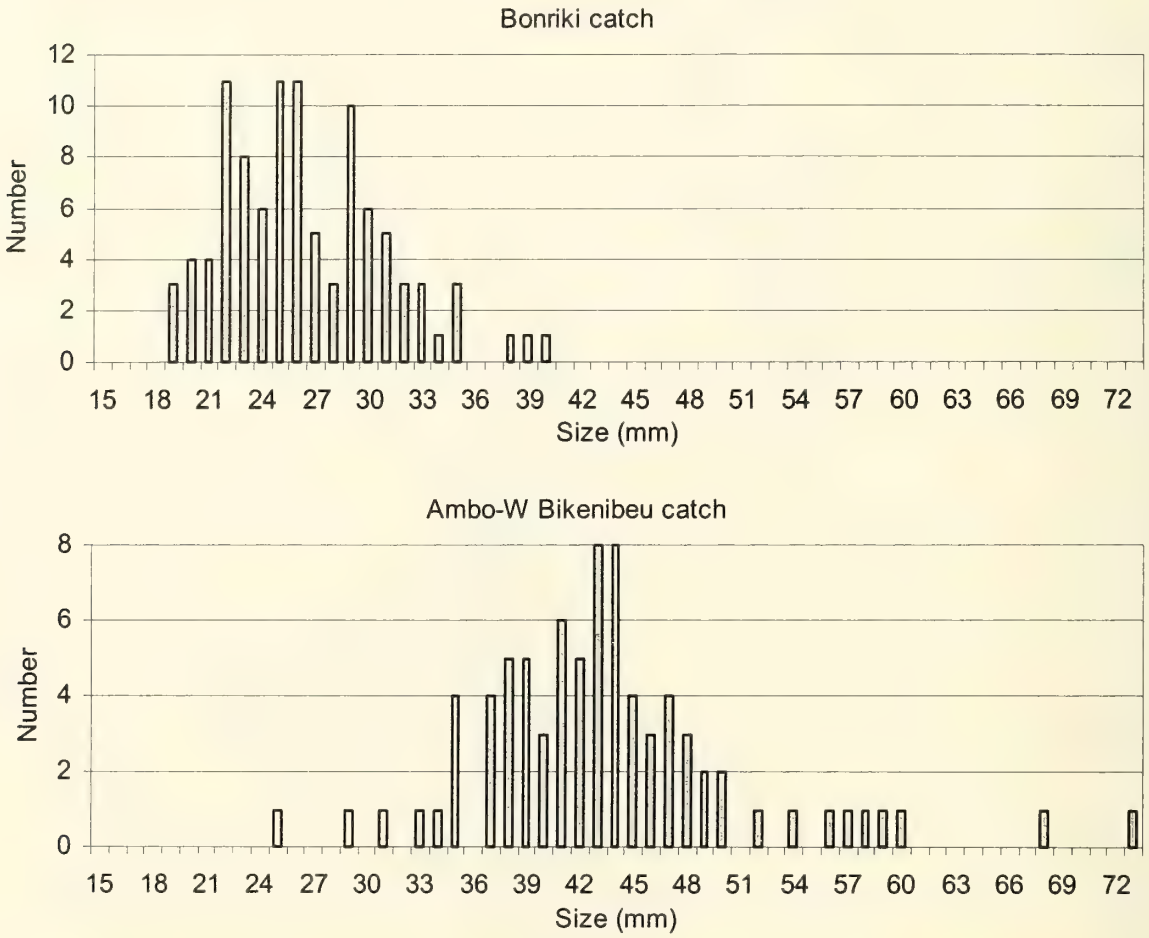

Figure 6. Size frequency distribution of *Anadara* in catches at Bonriki and at localities west of Bikenibeu. Based on N=20 clams sampled per catch in 5 and 4 catches respectively.

Population dynamics - persistence of beds

The observed spatial and temporal variability in recruitment suggests that recruitment limitation is important in structuring *Anadara* populations and could lead to fluctuations in resource abundance through time. The latter is supported by information gathered from older informants who indicate that *te bun* has undergone marked fluctuations in abundance over the past 50 years on several islands. The importance of variation in recruitment in structuring marine populations is increasingly recognized (Doherty and Fowler, 1994; Hughes et al., 1999), and can in extreme cases (as in the crown of thorns sea star, *Acanthaster planci*) lead to outbreak and crash cycles (Birkeland and Lucas, 1990).

The elders on both Abemama and Maiana Atolls recalled that *te bun* fluctuated considerably in abundance over past decades. During the 1920's *Anadara* was claimed to have "disappeared", while during the 1930's and 1940's it came back and was very

abundant. On Abemama *te bun* was again scarce during World War II, but became abundant again later. In the 1980's *te bun* was very scarce in most villages of Abemama, and was also rare on Maiana. Today *Anadara* has "disappeared" from Maiana but is still abundant on Abemama. In contrast *te bun* appears to have been fairly stable on Abaiang Atoll through living memory.

Te bun has been known in South Tarawa through living memory, although it is said to have become much more abundant in recent decades. *Te bun* boomed in abundance in South Tarawa after World War II, although it is also reported to have declined slightly in recent years (Johannes, 1992). *Te bun* is reported to be a recent colonist to North Tarawa, however, having appeared there only after World War II in the seagrass beds opposite the villages Buariki and Tearinibai. The massive recruitment of *Anadara* in the Bonriki area in 1993 documented above appears to be a new event because none of the people interviewed had seen the shellfish in abundance in that area in the past. It remains to be seen whether this represents an isolated or recurrent event and thus whether a *te bun* bed will become established in the area.

In addition to the apparently important role of recruitment variation in regulating *Anadara* abundance, environmental changes also can have large-scale effects on settled *Anadara*. Thus, Paulay (2001) found a major increase in the size of seagrass beds off South Tarawa following World War II, perhaps as a result of anthropogenic nutrient input from adjacent islets. This increase in seagrass beds may be partly responsible for the contemporaneous expansion of *te bun* resources in the area noted by Johannes (1992). On Marakei Atoll the formerly abundant *Anadara* is now disappearing. This may be attributable to the general closure of this atoll by the construction of a causeway across the main western passage of its highly enclosed lagoon.

The apparently large population fluctuations, whether due to recruitment dynamics or benthic processes, indicate that *Anadara* may be a somewhat unreliable resource in the long run. This hypothesis is supported by records of Holocene changes in *Anadara* abundance on other Pacific islands. In the Mariana Islands, *Anadara antiquata* was an important component of shell middens in southwest Saipan and northern Guam during the Pre-Latte period (ca. 3500-2000 BP) but disappeared from middens thereafter (Amesbury, 1999). Recent searches in northern Guam have revealed no evidence for the occurrence of *Anadara* in the area today (G. Paulay, pers. obs.). In contrast, in middens from southern Guam, *Anadara* gained prominence only during the past 500 years (Amesbury, 1999). Similarly, *Anadara antiquata* occurs in the Holocene of Aitutaki (Cook Islands), where (as well as elsewhere in the southern Cooks) intensive surveys failed to reveal any living individuals today (Paulay, 1996). *Anadara antiquata* also has undergone local extinction in the Hawaiian Islands since the late Pleistocene, and *Anadara uropigimelana* has disappeared from Niue since the Pliocene, albeit as a result of tectonic uplift at the latter (Paulay, 1996).

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ATOLL RESEARCH BULLETIN

NO. 489

I-KIRIBATI KNOWLEDGE AND MANAGEMENT OF TARAWA'S LAGOON RESOURCES

BY

R.E. JOHANNES AND BEING YEETING

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I-KIRIBATI KNOWLEDGE AND MANAGEMENT OF TARAWA'S LAGOON RESOURCES

BY

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ABSTRACT

Knowledge of the fishermen of Tarawa Atoll, Kiribati concerning some key food fish in their waters is described and shown to be highly relevant to the management of these fish. The bonefish, *Albula glossodonta*, has been the most important shallow-water finfish in Tarawa catches. However, all but one of its known spawning runs has been eliminated according to fishermen and this last remaining run is showing signs of severe depletion. Traditional marine resources management measures, some conservation-driven and others with different objectives, were diverse. But they have largely disappeared due, in part at least, to the impacts of British colonial rule. Reestablishing some form of local marine tenure seems essential to sound marine resource management, although the difficulties that would be encountered in doing so are not trivial.

INTRODUCTION

This report describes the results of an investigation of local knowledge concerning Tarawa's marine resources, as well as local customs relating to their exploitation and management. The study was part of a United States Agency for International Development (USAID)-funded project designed to assist in formulating a contemporary marine resource management plan for Tarawa Atoll. The study involved interviews with fishermen and other knowledgeable I-Kiribati throughout the atoll over a total period of three weeks between February, 1992 and October, 1993.

Informants deliberately were not randomly selected and we sought out individuals with high reputations in their villages for fishing expertise. For the most part these were people between 42 and 79 years of age. Some of them no longer fished because of physical infirmity, but all maintained an active interest in fishing and in the changes in fishing conditions occurring over the years. The attitudes and knowledge revealed by these interviews should not be assumed to be representative of Tarawa's fishing communities as a whole, but of their most experienced fishermen.

Our questions concerned the distribution, abundance and behavior of living marine resources observed by fishermen, perceived changes in these during their lives,

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presumed causes, and possible remedies in cases where the changes were seen as deleterious. We also asked about past and present village-based controls on fishing activities.

Interviews were deliberately unstructured. When unanticipated but promising subjects came up we pursued them with further questions, thus following any potentially instructive pathways along which the interviewees' knowledge seemed to be leading us. To minimize the constraints put on informants by the limitations of our own knowledge and preconceptions, we did not use questionnaires or a survey-style format. The latter are useful when pursuing well-defined and circumscribed questions; they are inappropriate, however, in exploratory interviews concerning specialists' knowledge where the interviewer is uncertain concerning what types of useful information may be forthcoming (Johannes, 1993).

Yeeting, an I-Kiribati fisheries researcher, acted as interpreter between Johannes and most informants. A few informants were at ease communicating in English. Interviews most often occurred at informants' homes. Occasionally groups of fishermen were interviewed in their maneaba (village meeting house). Interviews lasted from 20 minutes to about 2 hours, with several informants being interviewed twice. Each night the results of the day's interviews were transcribed using a laptop computer.

A number of students of Gilbertese culture have claimed that intense secrecy surrounds special knowledge, including important fishing knowledge (e.g. Sabatier, 1977). Our experience, however, suggests that such secrecy is either much reduced from what it once was, or never was as pronounced as is sometimes claimed. Our experience is more like Koch's. Koch (1986, p. xvii) stated, "the techniques of even simple processes related to the daily provision of food are regarded as "secret", although, on account of the limitations of the environment, the resources and the methods of using them have long since become widely known." Secrecy today seems to be associated mainly with ritual aspects of preparations for fishing, such as what to chant as one prepares the bait, and the locations of certain fishing spots. It did not appear to interfere seriously with the provision by informants of the kinds of information most relevant to our study.

Before describing the results of our interviews, we summarize here the scattered literature on traditional knowledge and management of reef and lagoon resources on Tarawa.

VILLAGE-BASED FISHING REGULATIONS

Historically marine resources were the only significant source of animal protein for the I-Kiribati. Consequently the islanders developed a host of fishing methods (e.g. Banner and Randall, 1953; Catala, 1957; Lawrence, 1977; Luomala, 1980; and Koch, 1986) and possessed detailed knowledge of their marine environments.

They also may have possessed a traditional marine conservation ethic (eg. Sabatier, 1977; Teiwaki, 1988; and Zann, 1990) - that is, an awareness of their ability to overharvest these resources plus a commitment to minimize the problem[3]. Lawrence (1977) noted "continued and largely successful efforts to regulate fisheries on the island (Tamana). These are not new or recent efforts but stem, according to our informants, from pre-missionary times." Teiwaki (1988, p. 41) states, "each island had its own rules about fishing; when to fish, how to fish and where to fish, and what should be done before, during and after each fishing expedition."

Sabatier (1977) notes that I-Kiribati had a large number of sea-food taboos relating to age, sex, totem or for the whole community (see also Grimble1933, 1989; Teiwaki, 1988; and Zann, 1990). Various other fishing regulations, also often in the form of taboos, were promulgated and strictly enforced. Punishment for not observing them included threatened supernatural sanctions, fines, removal of fishing rights and even death (e.g. Bobai, 1987). Public censure was also an effective deterrent. Such controls were already in decline in Grimble's time, however, and have since declined further (e.g. Turbott, 1949). Observance of a few totem-related seafood taboos were still professed, however, by certain individuals we interviewed on Tarawa in 1991-93.

It seems very likely that not all traditional controls were devised with conservation in mind. Regardless of their original purpose[4], however, a traditional control would have functioned as conservation measure where the tabooed species was, or was in danger of becoming, overexploited and if the taboo did not result in additional harvesting pressure being directed toward other more heavily exploited species.

Sea turtles, for example, were taboo to pregnant women and never eaten during times of war or crisis because of their "cowardly ways" and the possible assumption of such traits by those who ate them, or by their unborn children in the case of pregnant women (Grimble, 1933). This regulation apparently was not based on conservation needs but nevertheless exercised a sparing effect on species that are well-known for their susceptibility to depletion. However, we cannot be certain that such regulations did not arise because of an awareness among leaders of the need for conservation. In many, if not most cultures and religions, the probable reasons behind various prohibitions are often unstated, while spurious but more persuasive reasons are articulated. The threat of supernatural retribution, for example, has proven a more effective deterrent in many

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[3]Koch (1986, p. 9) states, however, "there appears to be hardly any attempt at a controlled regeneration of resources. In places the sipunculoidea are being wiped out without a second thought, young clams and other animals are gathered before they have reached the correct stage of growth, and hiding places are destroyed without regard for subsequent catches." There is nothing inconsistent with the two contrasting assertions. Examples of disregard for environmental limits coexisting with environmental wisdom can probably be found in many cultures. Indeed, many Western cultures today provide striking examples of both extremes simultaneously. The point we wish to make here is that a local conservation ethic can provide a valuable reference point when promoting conservation. If it is not present, as is the case in some fishing cultures (e.g. Johannes and MacFarlane, 1991) a major education campaign is necessary to provide it.

[4]Older men we interviewed said they suspected that resource allocation was a more important factor than conservation in the evolution of these controls.

cultures than the real consequences of undesirable activities.

As conditions changed after Western contact, I-Kiribati responded with new management regulations. For example, nylon gillnets, which were introduced to Kiribati in the late 1950s, were subsequently banned on a number of islands because they were considered to be "too efficient" (Tikai, 1980). Similarly, imported lures or local lures fitted with steel hooks were banned on several islands because they were also considered too efficient as well as damaging to the mouths of fish that escaped (Lawrence, 1977; and Tikai, 1980).

Other institutions also reduced pressure on some marine resources. For example, a variety of shallow-water invertebrates and algae were not eaten by choice, but reserved for consumption during times of hardship when fish were unavailable in sufficient quantities and as a form of "social security" for old people and other disadvantaged who could not fish (Zann, 1990).

For centuries, I-Kiribati have raised milkfish in specially constructed ponds (Catala, 1957). Green turtles were also raised with hand feeding in an enclosure on North Tarawa in the early 1980s according to Zann (1990). Zann (1990) points out that the designation of tunas as high-prestige fish has also helped redirect fishing pressure from limited shallow-water resources to functionally unlimited migratory pelagic stocks.

Some of the islands' customary fishing rules were embodied in the *Tuan Aonteaba* (Island Regulations) 1950, passed by the British colonial administration. These regulations were repealed in 1967, however, following the introduction of local government to the islands. Island councils were given the responsibility to control all kinds of fishing activities on their islands, but any council fishing bylaw had to be approved by the central government. Getting this approval proved to be an insurmountable obstacle until after independence in 1979.

Even then, according to Teiwaki (1988, p. 41), the central government was not "very receptive to the Island Councils' requests to pass certain fishing byelaws to protect the inshore fisheries and traditional fishing rights." The central government has become more receptive in the past few years, although the difficulty of reconciling the legal system and government policies adopted from colonial times with local regulations has slowed progress, just as it has in many other Pacific Islands (e.g. Zorn, 1991).

CUSTOMARY MARINE TENURE

Customary marine tenure (CMT) was the most important marine conservation mechanism in Kiribati and the foundation for most other fishing regulations. It gave tenure holders the right to exclude others from their fishing grounds. It underpinned villagers' marine resource management, providing them with the incentive to look after their marine resources by ensuring that they could retain for themselves the future benefits of doing so.

We focus here on the conservation value of CMT, but it should be stressed that, to islanders, CMT is much more than just a means of facilitating marine resource conservation. As Teiwaki (1992) pointed out, CMT "is the embodiment of the political, social, economic and psychological needs and responses of (Tarawa people) in relation to their marine environment." As elsewhere in the Pacific islands, it is not unlikely that CMT arose initially in Kiribati as a way of allocating marine territory rather than as a conscious marine conservation measure. Regardless of its origins, however, ownership of fishing grounds provides the essential foundation for conservation of marine resources.

On south Tarawa in precontact times, the island of Betio, now part of the Gilbert Islands' only urban center, was divided, according to Teiwaki (1988, p. 37) "into eight different *Kaingas*. A *Kainga* is a cluster of households with families living together for their own common interests. Each *Kainga* had its own plots of land and designated marine areas. A member of a *Kainga* might have fishing and other similar privileges in other *Kaingas* because of intermarriage, as a gift, or as a result of a *tinaba* . . . a special gift given to a woman who had provided sexual hospitality to a close male relative of her husband."

Teiwaki continues (p. 38), "...the size of a *Kainga* in precontact Betio was very small, consisting of not more than a dozen households with an average number of six people in a family. The population of the village was relatively small and there was no need to compete for the use of the sea amongst the village people, except in the case of aliens. *Nei Teba*, a rock formation about a mile eastward of Betio, was the designated maritime boundary between Betio and the next village, Bairiki. People from these villages could not extend their fishing or other sea-related activities beyond *Nei Teba*. It is understood that there was a passage named after a Bairiki person (Ten Taraia) who was killed by the Betio people because he was usually seen fishing beyond the boundary towards the Betio side."

Starting in colonial times, government action (and inaction) has contributed significantly to the decline of CMT and a consequent decline in the ability of villagers on Tarawa and elsewhere in Kiribati to manage their marine resources. In 1892 the Gilbert Islands became a British protectorate. At first the British colonial government, "allowed the customary sea tenure to prevail and ensured that the long-term fishing interests of the Kiribati people were protected from outside interests" (Teiwaki, 1988, p. 38). In 1946, Teiwaki relates, the first Fisheries Ordinance was initiated recognizing traditional fishing rights and making specific provision for the registration of these customary rights. The Native Lands Commission, which was responsible for registering land rights, also was empowered to deal with similar issues with respect to traditional marine tenure.

However, after the departure of a colonial official who spearheaded this initiative (the anthropologist, Harry Maude), little was done to follow through; no formal registration of marine tenure rights was ever undertaken. This was apparently because,

Teiwaki (1988, p. 38) states, the colonial administration favored the "principle of open access to fish anywhere and at any time irrespective of traditional norms. The local concept of marine rights was contrary to the British notion of public rights in the sea and its resources, the ownership of which were vested in the Crown or state." (It should be noted here that not only modern fisheries theory, but also the United Nations Convention on the Law of the Sea, constitute a sound global repudiation of this notion of the inherent "rightness" of open access, a principal that once held almost sacred status, not only in Britain but throughout the Western world).

Zann (1990) suggests another likely contributing factor to the decline of customary marine tenure. The British amalgamated small hamlets into larger villages on land chosen by the administration. The *utu* (extended families) who owned the fishing grounds adjacent to each hamlet were often relocated to areas distant from those fishing grounds. Goodenough (1963) attributed the decline to the increased use of canoes when imported timber became available and, therefore, greater emphasis on offshore fishing. This suggestion is unconvincing; many other Pacific Islanders, who were well-endowed with canoe trees and were expert in the art of offshore fishing (e.g. Hawaiians, Samoans), nevertheless maintained strict marine-tenure laws.

Traditional fishing rights were also seen to be obstacles to the implementation of government projects such as baitfishing by commercial tuna-fishing interests in once-tenured waters. According to Zann (1990, p. 89), on Tarawa, "former sea owners have prevented *Te Mautari* from collecting milkfish (*Chanos chanos*) fry for their baitfish aquaculture, but a confrontation between traditional interests and the national government was averted by the decision to pay villagers $5 per bucket of fry (Teiwaki, pers. comm.). Traditional owners of the lagoon floor at Ambo, on Tarawa, are complaining about an *Eucheuma* algae farm in their area, while those at nearby Bonriki are protesting the establishment of government milkfish ponds in their traditional waters."

Teiwaki (1988, p. 41) states, "the Island Councils were sensitive about the depletion of fishery resources in their vicinity because of the needs of their own people. There was no subscription to the government's argument that the fisheries resource was for the benefit of the public and not for the exclusive use of the people who were indigenous to a particular Council area." Teiwaki (1988, p. 25) also states that "certain Island Councils had managed to recommend to central government the institution of specific bylaws concerning the management of fishing activities within their own traditional fishing grounds. The ownership of fish traps had been previously registered in 1952 as part of the codification of land rights and ownership. Some islands, like Tabiteuea North and North Tarawa, have bylaws prohibiting fishing or sailing within a prescribed limit at a time of the fishing season (*te ikabuti*)[5]."

Other limited marine rights recorded by the government included ownership of fish traps, sea walls, accretions, reclaimed lands and fishponds. Unfortunately, as

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[5] *te ikabuti,* described in detail later in this report, refers to the phenomenon of the lunar periodic migrations of bonefish (*Albula* sp.) to spawn, a time when they are especially vulnerable to exploitation.

Teiwaki relates, "the registration of these rights . . . was made in the name of an individual, usually the male head of the *Kainga* or *te utu.* Although the registered 'owner' had customary obligations toward other members of the *Kainga* or *te utu,* the law did not specify this social requirement, causing considerable ill-feeling amongst the relatives. The effect of this was that the registered owners could be oblivious of social obligations towards their own kin. . . . . The Lands Commission should have arranged the registration of the recognizable marine rights under the joint ownership or trusteeship of the leading members in the *Kainga* or *te utu* to ensure the continuous access of those members to those rights." (Teiwaki, 1988, p 40).

Until the construction of causeways destroyed bonefish spawning runs, and goatfish spawning runs dwindled (see below), private ownership of traps constructed to catch these species was reported to be generally respected on South Tarawa. We could find no one who could remember a time when more general marine-tenure rights were practiced here.

Today the thousands of outer islanders who now live in South Tarawa place heavy pressure on nearby lagoon seafood stocks, especially shellfish. According to Teiwaki (1988, p.12), "the Tarawa landowners (*Kain Tarawa*) moan and complain about these (marine) foraging activities of the non-*Kain Tarawa* people (nonindigenous to Tarawa), but the government advised that the lagoon and its resources belong to the state and every I-Kiribati is entitled to harvest its resources. The Tarawa people argued that the shellfish grounds had always been a traditional source of food before the arrival of the British and other people from their outer islands. The village leaders had to be consulted before people from other places could collect the shellfish from their village. Failure to conform would result in a feud between the opposing parties. It would seem impossible for the Kiribati government to accept the complaints of the Tarawa people as it would mean that the individual islands could follow suit and claim rights over such shellfish. However, it is without doubt that the Tarawa landowners have become relatively disadvantaged as a result of their home island becoming the national capital."

Seaweed farming in shallow nearshore waters has waxed and waned in recent years in Tarawa Lagoon. Because the government does not recognize customary marine tenure, there are no restrictions on where farmers can raise their seaweed. This often has resulted in conflicts among seaweed farmers competing for the best places, and between seaweed farmers and fishermen. Vandalism has caused disruption of several farms. Teiwaki (1988, p. 28) states, "unless some amicable arrangements are made by the government and the lagoon users, the utilisation of the lagoon may be severely hampered."

A *de facto* form of marine tenure has replaced the old system in some areas. Teiwaki (1992) states, "In spite of their non-codification, traditional marine tenure is very much alive and respected in the rural villages." Local councils have thus limited access to certain fishing grounds to a particular village or island (e.g. Zann, 1990) despite the central government's unwillingness to formally sanction such actions.

In North Tarawa, where people remain somewhat closer to their original patterns of resource use than South Tarawa residents, some forms of customary marine tenure are still exercised today and others are remembered. The following presents a summary of our necessarily superficial investigation of the status of CMT today on North Tarawa. A more thorough study would require longer periods of more narrowly focussed interviews.

Traditional ownership by certain families was exercised over certain specific locations on the reef and in the lagoon in North Tarawa (see below). Seventy-seven-year-old, life-long Buariki resident and former North Tarawa senior magistrate, Ruka Kaburoro, told us that prior to British times, Buariki claimed ownership of adjacent waters. Because of the rich resources contained there in the form of bonefish and goatfish spawning runs, there was much fighting over locations for siting rock-fish traps. People were killed in arguments over these sites and certain rock traps are still identified today by the names of some of those individuals who died fighting over them.

The famed Arthur Grimble (later Sir Arthur), who was at one time British High Commissioner of the Gilbert and Ellice Islands, decided, according to Kaburoro, to try to end this disharmony. He proposed that the fishing grounds be divided between different Buariki families. Although this was done amidst much bickering, and allocations were decided as much on the basis of political clout as on equitability, Grimble's strategy worked and harmony (relatively speaking at least) prevailed on the fishing grounds.

When the British government first declared public ownership of most marine resources other than registered fish traps, some fishermen took advantage of this, according to Kaburoro, by refusing to observe the Grimble-inititiated allocations any longer, as well as the traditional exclusive right of Buariki people collectively over their fishing grounds. This attitude persists today, supported by various court decisions over the years discouraging villagers' efforts to control the activities of outside fishermen. Buariki villagers, however, have chased off outsiders gathering shellfish for commercial purposes on the lagoon reef flat in recent years.

Other north-Tarawa villagers told us that, traditionally, certain families or villages claimed exclusive fishing rights over particular sand banks or "rocky" (meaning coralline) outcrops in the lagoon where the fishing was good. The people of Nabeina, for example, had the exclusive rights to fish over certain banks and coral outcrops stretching as far as Bikeman Island, according to one informant. Here they used special sennet nets, hung with *te bun* shells as weights, to fish for jacks (carangids) and gerreids (silverbiddies). As at Buariki, observance of these fishing rights at Nabeina faded when the government declared its ownership of Tarawa waters.

LOCAL MARINE ECOLOGICAL KNOWLEDGE

The Literature

Pacific Island fishermen often possess knowledge concerning their marine resources unknown to fisheries biologists. Some of it can be invaluable in developing contemporary marine resource management programs. Unfortunately, the ethnographic literature dealing with indigenous marine environmental knowledge of I-Kiribati is unreliable. Grimble's descriptions of fishing and fishing lore cannot be trusted. Interspersed among descriptions that may or may not be accurate are absurd fantasies masquerading as true accounts, such as a description of how Gilbertese fishermen (and latterly Grimble himself) used themselves, tied to a rope, as bait to catch giant octopus (Grimble, 1952). Luomala, the only other ethnographer to devote significant space to Gilbertese fishing lore, was under the impression that sharks and rays have lungs, porpoises attack canoes (Luomala, 1984, pp. 1212, 1219, 1234), crabs have tails and groupers are toothless (Luomala, 1980, pp. 544, 549).

Local Knowledge: Results of the Interviews

Spawning Migrations and other Movements

Among the most useful local knowledge for purposes of marine-resource management in many Pacific Islands is that concerning the spawning migrations and aggregations of reef and lagoon fishes. A large variety of such species migrate along a highly regular route during a predictable season, moon phase and tidal stage. They aggregate at the terminus of this migration in order to spawn, then return to their prespawning areas (e.g. Johannes, 1981; and Thresher, 1984).

The spawning migrations of certain reef and lagoon fishes have been the focus of much fishing activity in Tarawa because they presented regular opportunities for making very large catches. Accordingly, fishermen were able to provide us with considerable information concerning some of these migrations. Fish engaging in such behavior are not only more accessible to fishermen, but they also offer biologists exceptional opportunities for monitoring stocks. Just as populations of salmon returning to their rivers to spawn are far easier to monitor than at other times, so many reef fish are easier to census when they are concentrated in their spawning runs. In addition, these runs provide a useful focus for the regulation of fishing pressure (Johannes, 1980; Sadovy, 1997; and Johannes et al., 1999). In Tarawa, fishermen have taken advantage of such spawning runs for centuries. So far, fisheries managers there have not.

Bonefish

Bonefish, or *te ikari,* is not only the most popular food fish in Tarawa but catch statistics show that it has also been the single most important species[6] in shallow-water catch and in commercial sales[7]. Sabatier (1977, p.121) observed in the 1930s that on some islands in the Gilberts, bonefish accounted "for perhaps half the fish consumed." Research elsewhere has shown that, after an oceanic larval stage, bonefish move into shallow water. Here they feed on invertebrates on sand or mud bottoms. They are found in Tarawa Lagoon over such bottoms. Although bonefish are found throughout the nearshore tropics and are a highly valued game fish in some regions, very little has been published concerning their reproduction. The descriptions of bonefish reproductive behavior given to us by Tarawa fishermen were highly consistent with one another and contained considerable information not to be found in the scientific literature.

Every lunar month, according to Tarawa fishermen, bonefish formed large schools one to three days before the full moon[8]. These aggregations (which we will refer to here as prespawning aggregations) formed in the lagoon near the spot where the fish would subsequently leave the lagoon on their spawning migrations. All but one of their reported migration routes involved passes between islands. The most important passes for bonefish migrations were Buota, Abatoa, Taborio, Tabonibara, the passes now blocked by Steward and Anderson causeways, and the Betio-Bairiki pass. The latter has been almost completely blocked by a causeway since 1987.

At low tide, bonefish entered the inner mouth of the interisland channels waiting to migrate to the ocean. When the tide rose and the water currents became strong in the channel, the fish moved laterally up into shallow, slower-flowing water at the edges of the passes and moved seaward. An important bonefish run, which did not use an interisland pass, was located near Buariki where the fish migrated across the reef southeast of the village.

The location for which we were able to obtain the most information on prespawning aggregations, and how I-Kiribati responded to them, was a spot in the lagoon near Buariki, called *Te Tao*. Traditionally an elder from Buariki was responsible for directing where and when people could place their nets during the bonefish spawning period. Great care was taken not to disturb prespawning aggregations and no one was allowed to fish, to sail on the lagoon in their vicinity, or even to make loud noises in the village. The reason given for this was that disturbing

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[6]There may be two species of bonefish, genus *Albula*, present in the Gilbert Islands (Shacklee et al., 1982). Lacking adequate information on this question, however, we will refer to Tarawa bonefish as a single species in keeping with Tarawa fishing statistics and reports. Often referred to in the literature as *Albula vulpes,* Tarawa's main bonefish species has been identified as *Albula glossodonta.*

[7]Bonefish appear to be more important as food in those islands in Kiribati with appropriate lagoon habitats than anywhere else we know of in its circumtropical range. This is due in part to its very high production rate in these lagoons, an apparent consequence of very high lagoon productivity associated with equatorial upwelling (see Kimmerer and Paulay, this volume). In addition, the infamous bones for which the species gets its English name are less prominent in *Albula glossodonta* than they are in the better known *Albula vulpes.*

[8]One fisherman said that occasionally the migration would start as late as one day after the full moon.

the fish at this time tended to break up and scatter them, making fishing for them subsequently much less successful.

Similar village rules prohibiting any activities that might disturb the fish during their prespawning aggregations were said to have been in force in other Tarawa villages. As discussed below, bonefish are exceptionally wary and easily put to flight by nearby disturbances. Fishing was allowed to start only after the aggregation began its spawning migration across the sand flat and outer-reef flat toward the outer-reef slope.

However, when the government declared lagoon resource public property (see above), the people of Buariki lost the ability to control these activities. Eventually, as a result, people started fishing over these prespawning aggregations before they began to move out.

On or about the day of the full moon, and starting around 4 p.m. and ending around 10 p.m. (i.e. in the period bracketing the high spring tide at Tarawa during this lunar period), the schools at *Te Tao*, as well as at least seven other locations around Tarawa, migrated seaward. At this time their gonads filled their body cavities.

Fishermen report that, in response to harassment by sharks, schools of bonefish reaching the ocean would hug the outer-reef edge and move up into shallow water on the outer-reef flat when the tide permitted. When the fish returned to the lagoon at the place they had left it, they were invariably spent, according to fishermen. In the lagoon their schools were said to be unusually easy to find for the next few days because they stirred up clouds of mud to a degree not seen at other times[9].

No one we interviewed, including divers who frequent the outer-reef slope, had ever seen bonefish spawn[10]. Fishermen surmise, however, that bonefish from throughout Tarawa converged seaward of the reef dropoff off the southeastern tip of Tarawa Atoll near Temaiku to spawn. Consistent with this is the fact that bonefish leaving the lagoon to spawn at Abatao, which is near Temaiku, typically returned after only one day, whereas, fish migrating from the lagoon at more distant locations, such as Betio and Buariki, typically returned after three days, according to fishermen.

There is additional evidence that the massing of bonefish takes place in this area during their spawning migration. The pass at Temaiku, which used to open to the ocean until about 30 years ago when it was closed by local landowners, never had bonefish runs according to fishermen. Nevertheless, the remains of the highest concentration of bonefish traps (see below) on Tarawa are located on the ocean-reef flat here. Since there was no bonefish run through the adjacent channel, the bonefish these traps were built to catch therefore must have migrated to this location from elsewhere. There is only one

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[9]Bonefish feed by grubbing in the sediment; perhaps they feed particularly heavily after spawning because their energy reserves have been depleted.

[10]Many reef and lagoon fish spawn during a short period around dawn or dusk, making observation difficult (Johannes, 1981; Thresher, 1984). Also, some Pacific Island fishermen do not recognize the spawning act for what it is when they see it (Johannes, 1989).

reason bonefish are known to migrate outside the lagoon, that is, to spawn.

Adding further plausibility to fishermen's hypotheses concerning where Tarawa bonefish spawn is the fact that spawning aggregations of a wide variety of tropical nearshore fishes are known to occur at outer-reef promontories such as the one near Temaiku (e.g. Randall and Randall, 1963; Johannes, 1978).

For centuries on Tarawa, bonefish returning to the lagoon after spawning were captured in rockfish traps built specifically for that purpose[11] at strategic spots on the outer-reef flats. Not uncommon were catches so large, we were told, that people could not harvest them all, with as many as 2,000 fish being gathered from a trap in one morning and the trap being full again by evening. A thousand fish in a trap was said to be a typical catch with as few as 400 being caught in "poor months". Some of the excess were salted. During their return from spawning, the fish would sometimes be so abundant and crowded on the reef that many would simply strand at low tide.

We are quoting from local fishermen here, and fishermen throughout the world have a reputation for exaggeration. However, fishermen from all over Tarawa volunteered the same quantitative information. A passage from a report by the famed Pacific Island ecologist, Dr. René Catala (1957, p. 132) lends further credibility to their statements. Here he describes bonefish fishing on Tarawa in 1951:

> "It is indeed exactly at the moment of the full moon that they approach the shore and that a great number of them get caught inside the traps without being incited to escape by the ebbing tide. Unlike mullet caught in this way, they do not jump over the walls; or when they try to do so it is too late. The fishermen are around the trap spearing them. The women carry them to the shore where the sharing is done in the shade of the coconut trees between the owner (of the trap) and the close relations and friends, a portion being left for the people who helped catch or carry the fish. . . . .The haul will vary in importance each month. We were fortunate enough to attend one of these distributions at the full moon of August. While not a record, the catch was nevertheless one of the best for the year, totaling over two thousand fish for one trap only. Only four hundred had been caught the preceding month, which was considered a very low figure. The weights we recorded gave a total of 45 pounds for twenty fish, taken at random. The largest weighed 4.5 lbs."

Catala (1957 pp. 122, 129) also refers to "massive concentrations of *teikari* (*Albula vulpes*) along the shores outside Tarawa Atoll" and "huge concentrations of *Albula* " at Tarawa. Sabatier (1977, p. 121) states that from rock fish traps "you can on occasion pick up as many as two thousand of them (bonefish)."

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[11]Catala (1957, p. 131) supports fishermen's descriptions of the specificity of these traps: "These property rights (over rock fish traps) are a real benefit only at the times when the ikari are caught. The rest of the time the catch is small and made up of the same very small species that anybody can gather on the reef flat daily."

Since Catala was a trained biologist, we assume that his sample was indeed random and that his estimated mean weight of a fish (2.25 lb) was thus reasonably accurate. We, therefore, can make a rough estimate of the harvest from these runs. Catala's and fishermens' statements both suggest that an average monthly catch per trap was about 1,000 fish weighing 2.25 lb each, or a total of about one ton. This amounts to 12 tons of fish per year, per trap (there are, in fact, 12.3 lunar months in a solar year).

This calculation does not include the bonefish that were caught by net fishermen during the spawning migration. Although the rock traps were privately owned, as were their catches, bonefish on spawning runs also were easily caught with nets by nontrap-owners, according to fishermen.

The remains of well over 150 bonefish traps are clearly visible today from the air on Tarawa's outer-reef flat. In the 1850s, Tarawa's population was estimated to be about 3,500 (Maude and Doran, 1966). If the 150+ bonefish traps were all in existence and operating simultaneously at that time, their catches alone would have provided about 1.5 kg of whole fish per capita, per day— a catch considerably in excess of their needs. It seems likely, therefore, that many of these traps were built in more recent times as Tarawa's population boomed.

Conditions have changed greatly in recent decades, however. Detailed interviews with expert fishermen throughout Tarawa revealed that by 1990 only one spawning run of bonefish remained — the one near the village of Buariki — and that it was declining fast. In addition, only five bonefish rock traps were still maintained on Tarawa, all of them at Buariki, and even these have now ceased to catch bonefish.

Some bonefish spawning runs began to dwindle in the late 1960s. Some were blocked by causeways (e.g. Tabonibara, Anderson, Stewart, and Taborio)[12]. More recently the Betio-Bairiki causeway, completed in 1987, destroyed what is said to have been the largest bonefish spawning run in Tarawa, apparently because the fish refused to go through the tiny pass (10 m wide) built into the 3 km-long causeway.

Fishermen say that the runs at Abatao and Buota passes dwindled and disappeared as an apparent result of localized overfishing. In the old days, bonefish would arrive at these passes in a few very large schools and were "as thick as baitfish." Imported gillnets began to be used intensively in and near these passes in the late 1950s to exploit the spawning runs. By the late 1960s, the fishermen noticed that the numbers of *te ikari* moving through these two passes were decreasing. In addition, instead of coming in a few large schools, the fish began to come in numbers of smaller schools. Then the runs began to miss a month, then two months. Then several months would go by without a run coming. Finally, about 12 years ago, the runs stopped entirely.
A decline in the numbers of migrating bonefish, presumed by fishermen to be due to overfishing, was also observed at the Betio-Bairiki pass prior to the elimination of this

[12]There were no suggestions from informants that blocked spawning aggregations sought egress elsewhere.

run by the causeway in 1987.

Buariki is the furthest village from the district center of south Tarawa. It is in one of the least heavily populated portions of the atoll and is one of villages least involved in commercial fishing. Perhaps for these reasons its bonefish run was the last on Tarawa to dwindle. Changes in the bonefish runs were not noted by Buariki fishermen until the early 1980s when the fish began to migrate in the form of many small schools rather than in a few very large ones as they did formerly. This is the same change in behavior as described independently by other fishermen for the other Tarawa spawning runs beginning in the 1960s before they ceased altogether. In addition, Buariki bonefish began to take a migration pathway further offshore in deeper water, out of reach of Buariki's five rock traps. Since about 1990 none of these traps—the last intact bonefish traps remaining on Tarawa — had caught any bonefish.

Since April 1992[13] the Buariki spawning run, the last known bonefish run on Tarawa, has failed to appear, according to fishermen. Occasionally since then small prespawning schools of bonefish formed at *Te tao* (see above). But these aggregations had become so small, and the fishing pressure on them so great, that no fish were seen to escape to complete the spawning run. These developments are of great concern to Buariki villagers who say that bonefish, along with *te maebo* (see below), have always overwhelmingly dominated their catch. They blame the decline mainly on "splash" gillnetting, which is described below.

Throughout the lunar month, large bonefish used to be caught on the lagoon side of Tarawa close to shore. By the early 1990s even small ones were not generally found there. Bonefish could still be caught in significant numbers in deeper lagoon waters, however, and in late 1993 were still frequently available from roadside fish sellers on South Tarawa.

Goatfish, *Upeneus* sp. (*te maebo*)

This goatfish is described by fishermen as making spawning migrations from the lagoon onto the reef flat on rising tides, and into the ocean as the tide drops, for three days around the new moon throughout the year. *Te maebo* do not migrate through interisland passes, but rather around the tips of the southernmost and westernmost islands on the atoll, Betio and Buariki. No one was able to tell us exactly where these fish spawn.

Low rock traps were used on the reef flat near the southern end of Betio specifically to trap this species during its spawning migrations. The traps are little used now because the migrations have dwindled to insignificance in recent years, according to fishermen. Overfishing, including the use of the splash gillnetting method (see below) is presumed by them to be the cause. For a few years before the catches diminished noticeably, many net fishermen moved into the area during the spawning

[13]Our interviews were carried out in 1992 and 1993.

run, placing their nets between the traps so that the fish had little chance of running the gauntlet.

Rockfish traps built specifically for *te maebo* are still used by the Buariki people on the reef flat to the west of the area where their bonefish traps are located. There are about 30 such traps and all of them remain in use. They are repaired periodically just before the new-moon spawning runs. The Buariki runs have also declined significantly in recent years, according to fishermen. In contrast to the bonefish near Buariki, *te maebo* now tend to run closer to shore during their migrations than they did in the past. Ten years ago a good catch would be up to 1,000 fish per night, per trap. By 1993, trap owners would be fortunate, we were told, to get 100 in a night. The mean size of the *te maebo* caught in the traps at Buariki, however, has not changed noticeably over the years, according to fishermen.

Goatfish, Mulloidichthys sp. *(te tewe)*

According to fishermen the goatfish, *te tewe*, made seaward spawning migrations through several channels in the early morning on a rising tide, often returning at the beginning of the same evening on the following rising tide. On their return they were described as travelling in small compact schools consisting of around 100 individuals. The biggest runs were said to be at Buota and Abatao passes. Both these runs are said to occur rarely now and consist of very small schools. Depletion is believed by informants to be the result of overfishing with gillnets. Runs were also destroyed by causeways at Tabonibara and Nuatabu, and, according to fishermen interviewed by Johannes (unpublished) in 1979, also by Anderson and Stewart causeways. A minor run reportedly still occurs at Kainaba. Information concerning the moon phases associated with these runs was inconsistent, although "around the full moon" was the most frequent description of their lunar timing.

Te tewe used to return from spawning in significant numbers via at least two channels (Tabituea and Nuatabu) not used by the species for outward migrations. Until the 1960s, *te tewe* could be caught in traps and with nets on the ocean reef at Nuatabu (a village near the pass of the same name, now blocked by a causeway, at the western end of Buariki Island), during which time they were full of eggs. A few days later small schools of *te tewe* would move from the ocean side through the channel in the evening as the tide rose. These movements continued until high tide each evening for three to five days.

We were unable to get an idea of how important these runs may have been as a source of food on Tarawa. Certainly they do not appear to have been as significant as bonefish or *te maebo* spawning runs, but important enough, nevertheless, to have prompted the building of specially designed rock traps along their migration routes at Nuatabu and Tabonipara and possibly elsewhere on the atoll.

Silver Biddy or Moharra, Gerres spp. (*teninimai*)

The silver biddy, *Gerres* spp., is said to come into shallower water to form large

schools in the lagoon over or around the edges of certain sand banks and islands around the period of the full moon.

The island of Bikenamori (literally "Island of the large silver biddies"), in the lagoon south of Tabonibara in south Tarawa, was often mentioned as the most important of such sites. A fish trap designed specifically to catch this species was said to have been once located there. There is a legend that Bikenamori belongs to a ghost called Bukamarawa who materializes as a light. *Teninimai* are "pets" of this ghost and are attracted by this light. The full-moon aggregation at Bikenamori was said to have become irregular in recent years. At this time the gonads fill the body cavity and the fish are easy to catch (with gillnets). Fishermen we talked with were unanimous throughout Tarawa in their assertions that, whereas numbers of these fish are still comparatively high, their average size has decreased dramatically and spawning aggregations have all but disappeared. These fish do not show up significantly in government catch statistics, but appear to form an important element of Tarawa villagers' subsistence catch.

Lethrinids and Lutjanids

Despite the fact that the spangled emperor, *Lethrinus nebulosus* (*te morikoi*), is the second most important species in shallow-water catches in Tarawa according to Fisheries Division data, we were unable to find out much about it from fishermen. The same is true of other popular, drop-line-caught lutjanids and lethrinids, including *te ikanibong*, *Lutjanus gibbus,* and *te rou*, *Lethrinus elongatus* All three species are said to have well-developed roe around full moon but are not believed even to school up to spawn, let alone leave the lagoon.

Many lethrinids and lutjanids are reported to migrate to outer passes or reef edges to spawn on lunar cycles in other tropical areas. Fishermen do not think they do this in Tarawa. In fact, fishermen we interviewed did not seem to know of any specific movements of these species, finding them mainly around rocky or coral outcrops in the lagoon. They said that it is becoming increasingly difficult to get good catches, although they are still to be had occasionally. The mean sizes of *te morikoi* and *teikanibong* are declining very noticeably, fishermen said, and some of their favorite fishing spots do not produce at all any more.

Mullets

Several species of mullet seem to be fairly important in catches in some parts of Tarawa today, according to fishermen. They were said to constitute the main replacement for depleted bonefish and *te tewe* runs in areas of North Tarawa (e.g. Abatao) where they are caught in deeper lagoon waters using a recently developed gillnetting technique.

Some informants told us that they had seen mullet in spawning aggregations around full moon off the point near Temaiku where bonefish are also believed to spawn (see above). Tarawa fishermen interviewed by Johannes (unpublished) in 1979 stated that the mullets *Liza macrolepis (te bauamaran*) and *Valamugil seheli (tebauataba)*

migrated from the lagoon to the ocean to spawn around full moon. According to these fishermen, such runs were restricted largely to channels along the eastern reef of Tarawa. Today all such channels are blocked, or nearly blocked, by causeways.

One informant said that mullet used to spawn in the lagoon near Temaiku before extensive dredging and filling disturbed the area. Another said that he had sometimes seen very large, compact schools of mullet six to seven miles at sea off Tarawa at the surface. Mullet were once seen in abundance during high tides on both the ocean reef near shore and in the lagoon near shore, but are no longer found in either location in significant numbers, according to fishermen.

Leatherskin

In 1979, fishermen told Johannes that the leatherskin, (*te nari*) *Scomberoides lysan*, migrated through the Betio-Bairiki channels to spawn five to seven days after the full moon. Similar migrations reportedly occurred near Buariki.

Sharks

Although I-Kiribati like to eat shark meat, fishermen did not provide much information on shark movements or aggregations, and sharks are not a common constituent of fishermen's catches today. Grimble (1952, p. 134) claimed that, "there is a four-fathom bank of Tarawa Lagoon where the tiger-shark muster in hundreds for a day or two every month," Their numbers were clearly visible from canoes, he said, and a few of them attained lengths of 18 feet. None of the fishermen we interviewed had heard of such a phenomenon. This could be because this shark aggregation was fished out as Tarawa's population grew. (Because of their low fecundity, shark populations are especially vulnerable to overfishing.) Another possible explanation is that this story is a product of Grimble's creative imagination (see below).

Whales and Porpoises

Whales and schools of porpoises once commonly entered Tarawa lagoon through Boat Passage according to fishermen. They often swam right into the Temaiku Bight area to a spot called *Uningan te kua*, meaning "Whale's Pillow" in Gilbertese. They were presumed by fishermen to do so because they could sense the fresh seawater coming into the lagoon in this area and therefore thought that they could get to the sea by swimming in this direction. This may account for the confused belief of some younger I-Kiribati that whales actually entered the lagoon through the pass connecting Temaiku Bight and the ocean. The pass was filled by adjacent landowners several decades ago. Prior to that time, however, it was never big enough to allow the entry of whales, according to an older informant. Inspection of the area supports this recollection.

Damaging Fishing Methods

Tarawa seems free of the twin scourges of many tropical-reef fisheries, dynamite and chlorine. A technique introduced in the early 1980s for driving fish into gillnets by splashing heavy six-foot crowbars into the water is a matter of considerable concern to many fishermen. The sound of these heavy bars penetrating a few inches into the water

when they hit it, scares bonefish more effectively than wooden rods which just smack the surface, according to fishermen.

The technique enables fishermen to scare fish from water deeper than that in which they can easily be gillnetted into shallower water where the nets are waiting. As mentioned above, fishermen believe that this method is responsible for important changes in the behavior of bonefish and *te maebo*. Feeling against the method ran very high among fishermen we interviewed in some parts of north Tarawa. In south Tarawa, even some fishermen who used the method told us they thought it should be banned.

DISCUSSION

Customary Marine Tenure

The above account of CMT in Tarawa is fragmentary and unsatisfactory, but it is the best that could be accomplished in the time available. When asked if it was reasonable to conclude that the current government's position on customary marine tenure was confused, one government official replied "chaotic would be a better word."

Teiwaki (1992) has expressed the need for a "remodelled" CMT system which, he says, "depends on an overall review of some government policies, particularly those related to the disruption of the marine environment or those policies that help to facilitate or accelerate the extinction of the traditional marine tenure system." (see also Teiwaki, 1988). We agree, and suggest that any such effort would require a more detailed study of the local traditional systems of fishing rights, and how they operated throughout Tarawa, than was possible in the time available during the present study. It would also require a detailed examination of the legal dimensions of the subject.

Kiribati government explicitly endorses a policy of decentralization yet does not support the keystone to decentralization of reef and lagoon resource management (CMT). I-Kiribati villagers have long demonstrated a desire to manage their fisheries. But today, although pressure on these resources by outsiders is significant, villagers have no authority to exclude them or control their activities and thus little incentive to regulate their own activities on the fishing grounds.

The resurrection, even in remodelled form, of CMT is bound to generate or reactivate boundary disputes and disputes concerning who has what traditional rights within bounded areas. We believe it is a price worth paying; it seems to be the only feasible way to implement sound management of reef and lagoon resources beyond South Tarawa. The expense and logistics of government management increase greatly with distance from administrative centers. Extensive consultation with a wide range of interested parties would be essential in order to minimize disputes and arrive at a satisfactory system.

Reestablishment of CMT in south Tarawa may be not be feasible because so

many of the residents are not traditional fishing rights owners. CMT- based management is often impractical near district centers (e.g. Johannes, 1998). In this case the responsibility must fall to the government. Government management is somewhat less difficult in areas in the immediate region of the enforcement agency because of simpler logistics.

Local Knowledge

As with many Pacific Islanders, the I-Kiribati of Tarawa possess valuable information about spawning migrations of important food fishes, including changes in their behavior and abundance as apparent consequences of human actions. Important information obtained during the interviews proved to be unknown to fisheries scientists and managers. Our study clearly demonstrates the value of appropriate interviews with selected fishermen as a means of obtaining practical information on the prior history of local fisheries where scientifically derived information is sparse. The most valuable information for management purposes was that concerning changes in bonefish behavior and distribution, the cessation of all but one known bonefish spawning run, and the severe depletion of the remaining run.

Clearly causeways have been responsible for the destruction of some of the spawning runs, and overfishing seems to have played an important role in eliminating others. It is worth stressing that, if village authorities had not lost their traditional right to exclude outsiders from their fishing grounds, some almost certainly would have prohibited practices such as splash fishing and blocking passes with nets during spawning runs.

As mentioned earlier, fishermen say that while splash fishing catches more bonefish in the short run, in the long run, it "spooked" the fish causing migrating schools to break up and, in the case of Buariki, causing the fish to shift their migration path to deeper water. How plausible are these assertions?

Tests carried out by Tavolga (1974) on a single specimen of *Albula vulpes* indicated unusually acute hearing at low frequencies (between 100 and 300 Hz). He also pointed out that bonefish are notorious among sport-fishing guides for taking flight in response to very small noises. In the field Tavolga determined that, by hitting an oar lightly against the gunwale of a boat or by dropping a lead sinker into the water, the resulting noise had most energy around or below 300 Hz, i.e., where the bonefish has its greatest sensitivity. The resulting noise level was above the animal's hearing threshold at 10 m from the source. He also noted that bonefish are often more "spooky" at depths of over 3 m than at 1 m or less. In this connection it is worth reiterating that Tarawa fishermen say they are targeting bonefish in deeper lagoon waters when using the splash-fishing method. Bonefish also produce a "startle-type" sound when disturbed (Myrberg, 1981) which may function to spread alarm, caused by splash fishing, to fish beyond the direct reach of the sound of the splashing.

Observations and measurements made elsewhere therefore support Tarawa fishermen's contention that splash fishing "spooks" bonefish. But what of their contention that the Buariki fish have altered their spawning migration pathway, now using deeper water in an apparent response to heavy splash-fishing pressure? Such behavior would entail learning, both to avoid the "noxious stimuli" (as behaviorists might describe splash fishing) along the old pathway, and to adopt, as a group, an alternate migration pathway. That bonefish, like many other fish, learn to respond negatively to sounds is demonstrated by Tavolga's experiments; his hearing tests on bonefish were based on a type of learning known as conditioned response.

How would new recruits learn the new migration path? The same way they probably learned the old migration pathway from experienced adults. No relevant research has been done on bonefish, but such learning of migration routes by novice fish from experienced fish has been confirmed for another tropical nearshore species,[14] the Caribbean grunt *Haemulon flavolineatus* (Helfman and Schultz, 1984). In short, what we know about the behavior of fish, including bonefish, provides no information inconsistent with fishermen's assertion that splash fishing has altered bonefish spawning migration pathway and behavior.

As mentioned earlier, Buariki fishermen say that bonefish in their area now no longer make spawning migrations, even in deeper waters, because their small and increasingly rare prespawning aggregations are eliminated by fishing before they can migrate. If bonefish learn to alter their migration pathways, however, the possibility remains that some have developed one or more alternative migration routes in Tarawa that are unknown to fishermen. It seems unlikely that this could occur in such a heavily fished lagoon, but the possibility cannot be dismissed. It is obviously prudent to assume that this has not occurred, however, and that if the Buariki spawning run cannot be reestablished, Tarawa may lose its *te ikari* entirely within a few years.

Large bonefish used to be readily caught in shallow lagoon waters close to shore according to fishermen, but even small bonefish are uncommon there now. Large bonefish are still caught in sizeable numbers in deeper waters in the lagoon (Beets, this volume). This tends to reduce the concern of some I-Kiribati over the fate of their bonefish stocks. But the observation is not as reassuring as it might appear. For one thing, the sex ratio of these fish is now heavily biased towards males (Beets, this volume). In addition, if Tarawa bonefish live for up to 12 years like their Caribbean counterparts (Bruger, 1974), there will be some bonefish in the lagoon, even in the absence of spawning (barring their complete removal by fishermen) for at least 12 years after the last known spawning, that is, until about 2004. We would, however, expect them to become increasingly uncommon before then due to natural and fishing mortality.

Some recruitment of bonefish larvae to Tarawa Lagoon from spawnings at nearby atolls may occur, but it cannot be taken for granted. If it does occur, it would

[14]It has been repeatedly demonstrated in migrating birds.

suffice to maintain adequate stocks. In addition, bonefish spawning runs are said to be seriously threatened on at least some of these other atolls, for example at Abemama (Tebano, 1991; and Siwau Awira, Kiribati Minister of Education, pers. comm.).

We thus conclude that Tarawa's single most important species of lagoon food fish could suffer local extinction unless concerted action is taken quickly to protect and rebuild the Buariki spawning run. Scientific proof of the seriousness of the situation is lacking, but would be expensive and very time consuming to obtain. In our opinion, waiting for such proof is a risk that the I-Kiribati can ill afford.

The total protection of any prespawning aggregations of bonefish that may form near Buariki seems critical. The banning of splash fishing seems desirable despite the absence of proof that it is as harmful as Tarawa fishermen believe it to be. In addition to the possible benefits of such an action discussed above, the banning of this method would appear to result in the *de facto* creation of a reserve in the deeper waters of the lagoon where bonefish would be out of reach of net fishermen altogether. Such a ban, as suggested by fishermen, also could help rebuild spawning runs of the goatfish, *te maebo* and perhaps other species.

ACKNOWLEDGMENTS

We thank the fishermen of Tarawa, whose knowledge is the foundation for this report. We also acknowledge the valuable counsel provided by Roniti Teiwaki during this study. Our research was supported by the U.S. Agency for International Development.

Note: Since this report was presented in Tarawa in 1994, steps were taken to protect the bonefish spawning run near Buariki. In 1995, the people of north Tarawa established and enforced an informal ban on fishing for bonefish in north Tarawa waters during the three days either side of the full moon. They also banned the use of long gillnets and the splash method to catch bonefish. This latter ban was officially recognized by the central government in 1999. In 1999, fishermen reported that the catch-per-unit effort and the average size of bonefish were both increasing. There were also unconfirmed reports of a bonefish spawning run being seen outside the reef of south Tarawa.

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ATOLL RESEARCH BULLETIN

NO. 490

DECLINES IN FINFISH RESOURCES IN TARAWA LAGOON, KIRIBATI, EMPHASIZE THE NEED FOR INCREASED CONSERVATION EFFORT

BY

JIM BEETS

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Figure 1. Map of Tarawa Lagoon, Kiribati, showing the eight fisheries-independent sampling sites used during the 1992-93 study. The center of the atoll (near station 5) lies at approximately $1^{O}27.5'N$, $173^{O}E$.

DECLINES IN FINFISH RESOURCES IN TARAWA LAGOON, KIRIBATI, EMPHASIZE THE NEED FOR INCREASED CONSERVATION EFFORT

BY

JIM BEETS[1]

ABSTRACT

The very productive lagoon fisheries of Tarawa atoll changed greatly in recent decades as human development and intensive harvesting increased. Tarawa typifies the increasingly common condition of resource depletion and marine community structure change with expanding human activities and population growth. Fisheries-dependent reports have documented the change in fisher landings for nearly two decades. A comparison of fisheries-independent data collected during 1992-93 with data collected in 1977 allowed for documentation of large changes in important finfish resources in Tarawa Lagoon. The historically important bonefish (*Albula glossodonta*), like other important fishery species, demonstrated declines in catch-per-unit effort (CPUE), proportion of catch, mean length and weight (1977: 46.4 cm, 1.31 kg; 1992-93: 37.6 cm and 0.84 kg), and sex ratio (1977: 0.71:1 [F:M]; 1992-93: 0.15:1). Beach seine sampling of bait fishes demonstrated a major shift in species composition between 1977 and 1992-93, with severe depletion of some preferred species. These results suggest declining abundance in locally important fish species and large changes in species composition within Tarawa Lagoon.

INTRODUCTION

The marine resources of Tarawa atoll (the economic and political center of Kiribati) have been relatively well studied. The benthic invertebrate resources are very productive and are intensively harvested (Paulay, this volume). Traditional marine knowledge and management has been documented by Johannes and Yeeting (this volume). These studies and numerous earlier investigations documented the large changes in lagoon resources as development, exploitation, and human population growth expanded, especially along the southern portion of Tarawa atoll.

Fisheries data and analyses of Tarawa Lagoon resources have documented declines in abundance in some areas of Tarawa atoll and have presented generally negative trends in yield and CPUE (Cross 1978, Marriott 1984, Mees 1987, Mees 1988 a, b, Mees et al. 1988, Wright and Yeeting 1988). Several fish aggregations and migrations have ceased and or changed migration patterns (Johannes and Yeeting, this volume). The predominant causes appear to be habitat alteration/loss and overfishing.

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The profile of the Tarawa Lagoon fishery greatly changed with an increase in the use of monofilament gill nets and boats with outboard engines, which coincided with the decline in use of traditional fishing methods. This resulted in an increased effort and landing of species selected by gill nets. With the high incidence of ciguatera on the outer reef of the atoll (McCarthy and Tebano 1988), fishing effort outside the lagoon has primarily targeted tuna or flying fish. Since offshore fishing around Tarawa is primarily a commercial effort using larger boats, most of the artisanal effort is on lagoon resources, although it is difficult to evaluate the proportion and importance of each from available statistics. In 1976, 87 outboards and 526 fishing boats were in use in Tarawa compared with 426 outboards and 1,312 boats in use in 1987 (Wright and Yeeting 1988). Although landings have continued at relatively high levels for Tarawa, CPUE of lagoon resources declined in recent years. Details of the fishery, such as declines of specific groups or species and changes in species composition of landings, are not provided in available reports; however, data analyses described a collapsing fishery in the lagoon.

The rapid human population growth on Tarawa atoll has placed increasing pressure on lagoon resources. The population is largely dependent on the lagoon resources for sustenance, and although lagoon resources have been traditionally used and preferred, a few investigations have evaluated the potential of other available resources. Two projects conducted by the South Pacific Commission, Outer Reef Artisanal Fisheries Project and Deep Sea Fisheries Development Project, demonstrated good catch rates for outer- and deep-reef resources (Crossland and Grandperrin 1980, Taumaia and Gentle 1983). These resources have incurred slight fishing pressure around Tarawa but are also susceptible to overfishing.

The presence of ciguatera has greatly restricted the use of outer-reef finfish resources around Tarawa atoll (McCarthy and Tebano 1988). There appears to be no incidence of ciguatera from fishes caught within the lagoon. The incidence of ciguatera around Tarawa atoll is apparently cyclic, not persistent. Use of outer-reef resources of the atoll could assist in removing fishing pressure from the lagoon; however, without rapid, inexpensive tissue tests, documentation of the decline of the incidence in ciguatera and identification of "safe" fish are not presently possible.

Additional resources and imports may become increasingly important for Tarawa, but, regardless, lagoon resources are important and preferred by Tarawans and thus require management. One goal should be the development of management strategies for sustainability of finfish resources within the lagoon. This goal requires adequate resource evaluation. This study component was designed to provide an evaluation of finfish resources in Tarawa Lagoon using historical data, fisheries-independent sampling, and fisher-landings surveys.

METHODS

An excellent description of Tarawa atoll, reasons for its high productivity, and documentation of benthic invertebrate resources have been presented by Paulay (this volume). The focus of this study was an evaluation of finfish resources of Tarawa lagoon; therefore, samples of fishers and fishes were restricted to the inner lagoon (Fig. 1). Data were obtained using two primary sampling methods: fisheries-independent sampling using gill nets, handlines, and seines, and fisheries-dependent sampling of fisher landings. Sampling for this study commenced in April, 1992 and terminated in February, 1994.

Gill-net and handline sampling

Fisheries-independent sampling was designed to assess finfish resources throughout the lagoon and for comparison with historical data collected in 1977. Gill-net sampling procedures were designed following those described by Cross (1978) to allow for statistical comparisons. Gill nets of the same mesh size and length were fished using the same set procedure and soak times. Only data from the same area fished in 1977 (Fig. 1, sites 6 and 7) and net mesh sizes (3.5 in [8.9 cm]) were used for the comparative analyses. Sampling was scheduled for three nights per month at one of eight permanent stations based on Global Positioning System (GPS) positions (Fig. 1). The randomized sampling schedule was devised based on eight sampling stations, four lunar phases, and four solar seasons. At each station, four gill nets were set at least 100 m apart, adjacent to shallow patch reefs or shoals that were present throughout the lagoon. Net dimensions were 50 m by 2 m, two nets with 6.4 cm stretch mesh and two nets with 8.9 cm stretch mesh. Each net was set from shallow water to deep (2-8 m) with lead lines along the bottom. Normally, two sets per night were made with soak times of three hours.

Handline fishing was conducted during gill-net sets with standard soak times. Each sampler used standard gear (30 lb. test monofilament, No. 9 hooks, leads) and fished in the same manner. Bait was standard juvenile milkfish (*Chanos chanos*) obtained from the Kiribati Fisheries Division fish farm.

During all sampling, parameters (date, time, site, lunar phase, climatic/physical conditions) were recorded by field technicians into field notebooks. Catch from each gear type was placed in separate, marked bags and processed in the laboratory. Data recorded on each specimen included fork length in cm, weight in grams, sex, and gonadal condition. Training and quick identification sheets for all species collected allowed for accurate species identification.

Seine sampling

Seine sampling followed the design of the previous study conducted by the Kiribati Fisheries Division (Cross 1978). The seine (50 m x 2 m x 10 mm stretch mesh) was hauled by four men from approximately 50 m offshore onto the beach. Fishes from each seine haul were labeled and returned to the laboratory for identification and measurements. Samples were taken in each of four major areas: North Tarawa, South Tarawa, Betio, and Bikeman. Bikeman later was eliminated from sampling due to the dramatic habitat alterations on that island since the last study. North Tarawa received low sampling effort (n = 4 seine hauls) and was not included in analysis.

Fisher Landings

The sampling design for finfish landings was randomized under given logistical and statistical constraints (Mackett 1973, Bazigos 1974, Ulltang 1977, Caddy and Bazigos 1985, Caddy and Sharp 1986). Fishers were sampled at randomized sites and dates, at least one day per week, with additional samples scheduled as possible. All samples were taken along the road which runs across the southern portion of the atoll (no road extended from the southeastern to northern portion of the lagoon). Samplers waited at a site to intercept all fishers landing within the defined time. Data were recorded on date time, gear type and amount, boat type, fishing area, landing area, fishing/soak time, sample type

(complete/partial catch), and climatic conditions. All fishes were identified by species, measured to the nearest 0.1 cm, and weighed to the nearest 0.5 g.

Bonefish (*Albula glossodonta*) was identified as a species of special concern and received additional sampling effort. Bonefish, greater than 35.0 cm (apparent size of maturity based on preliminary samples) in fisher landings, were separated for determination of sex and gonadal condition and for diet analysis.

RESULTS

Gill-net and handline sampling

During the fisheries-independent gill net sampling in 1992-93, 64 species were captured in 255 net sets. Paddletail snapper (*Lutjanus gibbus*) was the most commonly captured species (24.9% of total number of fish in gill-net sampling) followed by bonefish (*Albula glossodonta*, 7.5%; Table 1). Bonefish was the dominant fish captured in gill nets of the same mesh (3.5 in) during the 1977 investigation and represented a much larger proportion of the catch (44.6%; Table 1). Paddletail snapper was caught in similar proportion in both the 1977 and 1992-93 sampling. Several species, primarily snappers (Lutjanidae) and emperors (Lethrinidae), were common in 1992-93 gill-net sampling but absent in 1977 sampling (Table 1). Other taxa, especially squirrelfishes (Holocentridae) and trevallies/jacks (Carangidae), were abundant in 1992-93 gill net sampling (10.4% and 8.8%, respectively) but uncommon in 1977 samples (0% and 3.3%, respectively).

Table 1. Comparison of dominant taxa in fisheries-independent gill-net sampling, 1977 and 1992-93, and with fisher landings data. Data are percentages of total number of fish sampled. 1977 data from Cross (1978). Kiribati names are given beside common names.

	GILL-NET SAMPLING				FISHER LANDINGS	
	1977		1992-3		1992-3	
TAXON	Number	Weight	Number	Weight	Number	Weight
Albula glossodonta Bonefish - IKARI	44.6	66.5	7.5	12.9	41.0	61.3
Lutjanus gibbus Paddletail snapper - IKANIBONG	25.0	11.3	24.9	14.0	9.2	4.7
Gerres spp. Silverbiddy - AMORI	7.6	3.4	4.8	1.86	10.2	1.2
Lethrinus nebulosus Spangled emperor - MORIKOI	5.4	6.7	0.4	1.6	1.0	2.2
Lutjanus fulvus Flametail snapper - BAWE	0	0	6.6	3.4	6.2	2.7
Lethrinus obsoletus Orangestriped emperor - OKAOKA	0	0	4.4	2.4	6.6	3.5
Lethrinus olivaceus Longnose emperor -TAABOU/ROU	0	0	5.3	5.0	2.8	5.3
OTHERS	17.4	12.1	45.9	58.8	23.0	19.1

CPUE differed significantly between the two sampling periods, 1977 and 1992-93 (MW-U, $p = 0.002$). Average gill-net catch per net set (CPUE) for 3.5-inch stretch nets at the same location used in the 1977 study (Cross 1978) was 7.08 ± 5.45 (s.d.) fish per net set in 1977 and 1.57 ± 2.10 (s.d.) fish per net set in 1992-93 (Table 2). Large differences in CPUE were also noted for dominant species, especially for bonefish (MW-U, $p < 0.001$).

Table 2. Comparison of CPUE for total fishes and important species in fisheries-independent gill-net sampling in Tarawa Lagoon, 1977 and 1992-93. Data are mean CPUE (± s.d.) for 3.5-inch gill-net sets in 1977 (n=13) and 1992-93 (n=37) within the same area. 1977 data from Cross (1978). Kiribati names are given beside common names.

	1977		1992-93	
TAXON	**Number**	**Weight**	**Number**	**Weight**
TOTAL FISHES	7.08 ±5.45	6.20 ±5.50	1.57 ±2.10	0.92 ±1.52
Albula glossodonta Bonefish - IKARI	3.15 ±4.39	4.14 ±5.19	0.16 ±0.83	0.16 ±0.86
Lutjanus gibbus Paddletail snapper - IKANIBONG	1.77 ±2.77	0.70 ±1.15	0.78 ±1.70	0.31 ±0.67
Lethrinus nebulosus Spangled emperor - MORIKOI	0.38 ±0.65	0.42 ±0.76	0.03 ±0.16	0.07 ±0.41

Snappers (Lutjanidae), emperors (Lethrinidae), and groupers (Serrandae) dominated handline catches in the fisheries-independent sampling (as in the fisher landings) during 1992-93. A total of 54 species and 1,793 individuals were captured in 46 samples (approx. 560 fishing hours). Paddletail snapper (*Lutjanus gibbus*) was the most abundant species caught in handline sampling (39.8% of total number of fish caught), followed by orangestriped emperor (*Lethrinus obsoletus*, 17.6%; Table 3). Similar observations were made for the handline fisher landings. Trevellies/jacks and squirrelfishes were also important in landings; however, fisher catches of squirrelfishes may be much larger and not as apparent in landings since they are less preferred.

For both gill-net and handline sampling, catches were significantly greater in northern and western lagoon sampling sites (Sites 1, 3, and 4) than in southern and eastern sites (Sites 2, 5-8; KW tests, $p < 0.01$; Fig. 2 and 3).

Beach seine sampling

Thirty-eight species were sampled in 40 beach seine samples taken in Tarawa Lagoon in 1993, which was comparable to 40 species sampled in 176 seine samples taken in 1977. Comparison of the results between the two sampling periods demonstrated that the species composition and relative abundance of fishes captured using this method has greatly changed (Table 4). Several previously abundant species, primarily baitfishes, were not captured during seine samples in 1993. The second most abundant species captured in 1993, Dussumieri's halfbeak (*Hyporhamphis dussumieri*; greater than 20% of fishes captured), was rare in 1977.

Table 3. Comparison of six dominant species in fisheries-independent handline sampling with handline fisher landings data, 1992-93. Data are percentages of total number of fish sampled. Kiribati names are given beside common names.

	HANDLINE SAMPLING		FISHER LANDINGS	
SPECIES	Number	Weight	Number	Weight
Lutjanus gibbus Paddletail snapper - IKANIBONG	39.8	29.8	27.5	18.9
Lethrinus obsoletus Orangestriped emperor - OKAOKA	17.6	17.4	15.6	11.0
Lutjanus kasmira Bluestriped seaperch - TAKABE	8.8	3.3	4.5	1.0
Epinephelus merra Dwarf spotted rockcod - KUAU	7.3	3.3	2.9	1.7
Lethrinus olivaceus Longnose emperor -TAABOU/ROU	6.9	13.7	6.8	20.5
Lutjanus fulvus Flametail snapper - BAWE	5.0	2.5	8.6	3.2
OTHERS	14.6	30.1	34.1	43.7

Table 4. Comparison of results of inshore seine samples taken in Tarawa Lagoon, 1977 and 1993. Data are percentage of total fish captured for six dominant taxa in two areas, South Tarawa and Betio, 1977. Data from Cross (1978). Kiribati names are given beside common names.

	SOUTH TARAWA		BETIO	
SCIENTIFIC/COMMON NAME	1977	1993	1977	1993
Atherinomerus lacunosus hardyhead silverside - REREKOTI	33.14	1.36	15.79	0
Herklothsichthys quadrimaculatus gold-spot herring - TARABUTI	22.31	0.97	13.2	0
Gerres argyreus silverbiddy, mojarra - NINIMAI	14.62	32.61	1.07	7.93
Spratelloides delicatulus blue sprat - AUAN	13.07	0	8.37	0
Hypoatherina ovalaua Ovalaua silverside - REREKOTI	11.15	1.53	7.36	0.04
Mugilidae mullets - BAUA, BAUAMARAN	1.87	2.56	0.07	0.99
Number of samples	47	25	43	11

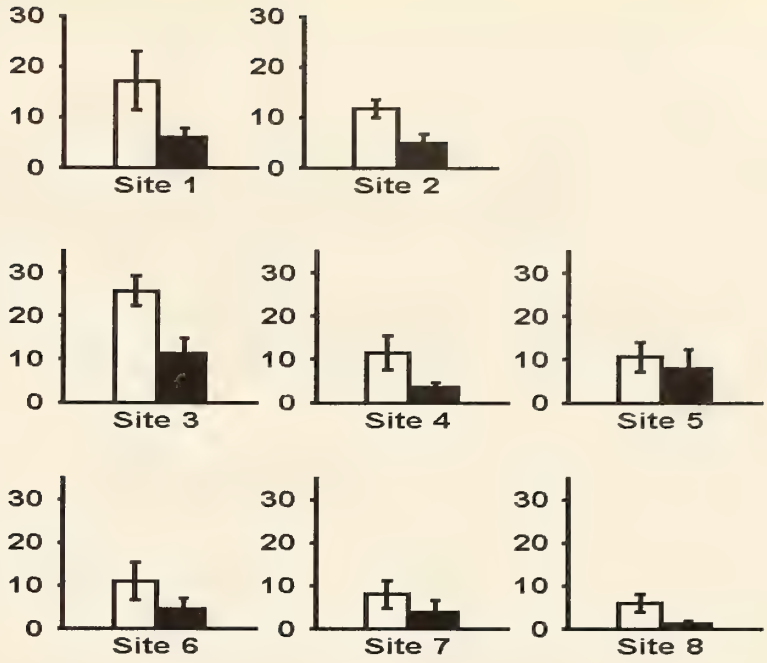

Figure 2. Mean number of fish (open bars) and mean weight in kg (solid bars) per gill-net sample for each sampling site in Tarawa Lagoon. Error bars are one standard deviation.

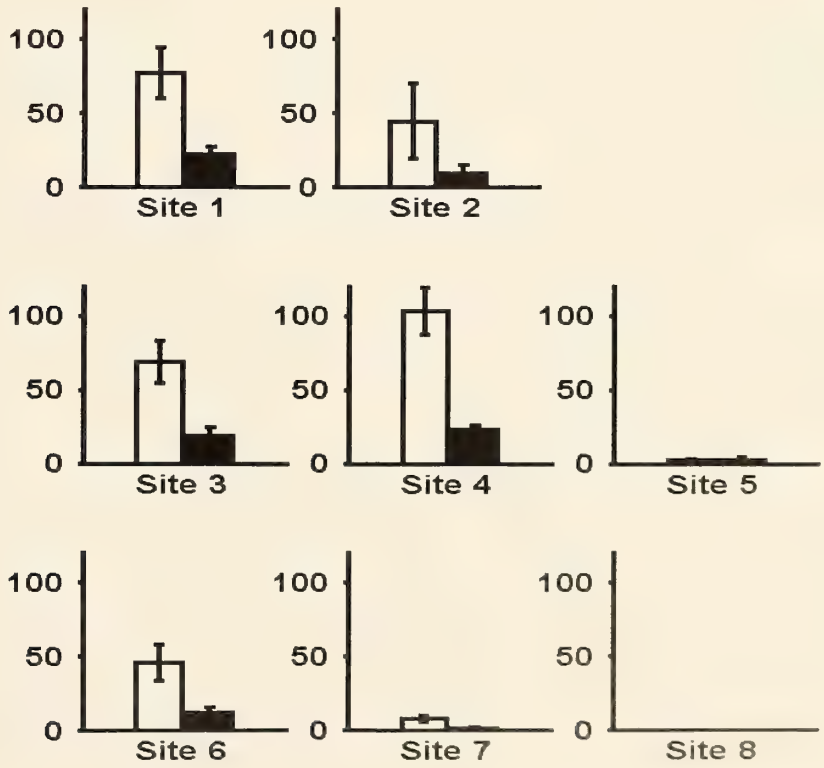

Figure 3. Mean number of fish (open bars) and mean weight in kg (solid bars) per handline sample for each sampling site in Tarawa Lagoon. Error bars are one standard deviation.

Fisher landings

Fisher landings surveys (n = 82) showed that bonefish dominated fisher landings (41.0%), followed by silverbiddies (*Gerres* spp.; Table 1). Bonefish landed by fishers were exclusively caught using gill nets. Fisher landings were reported for all gears because many fishers used several gear types per trip. Snappers (Lutjanidae), emperors (Lethrinidae), travallies/jacks (Carangidae), and goatfishes (Mullidae) followed bonefish and silverbiddies in abundance in fisher landings. The dominant fishes landed by handline were snappers and emperors (Table 3).

Gill-net fishers, who were sampled during landings surveys and target bonefish in Tarawa Lagoon, almost exclusively used the "splash method" of fishing gill nets (usually less than 100 m long) due to low catch rates using passive methods of fishing gill nets (see description of fishing methods in Johannes and Yeeting [this volume]). In the "splash method" fishers slap the water surface with long rods, which drives fish into the nets and enhances catches. Silverbiddies and goatfishes were also captured by gill net, whereas, reef species, such as snappers and emperors, were primarily taken by handline.

Bonefish data

At least two species of bonefish occur within this region of the Pacific (Shaklee and Tamaru 1981, Myers 1991). Meristic counts of bonefish obtained from fisher landings and fisheries-independent sampling were usually in the range of those given for *A. glossodonta* [although Cross (1978) listed *A. neoguinaica* for bonefish in Tarawa Lagoon]. Although two species may exist in Tarawa, for purpose of this report bonefish will be referred to a single species, *A. glossodonta*.

The mean length and weight of bonefish sampled in gill net sampling in 1992-93 (37.6 cm and 0.84 kg, respectively) were significantly smaller than those sampled in 1977 (36.4 cm, 1.31 kg), females (t-test, $p < 0.01$; Table 5). This was also true for the mean length of males and females (t-tests, $p < 0.01$; Table 5). The sex ratio was also greatly skewed between sampling periods (1977: 0.71:1 [F:M]; 1992-3: 0.15:1) Interestingly, the smallest reproductive individuals for both sexes sampled in 1992-93 were smaller than those sampled in 1977 (Table 5).

Comparison of length-frequency data for bonefish collected in 3.5-inch stretch gill nets during 1977 and 1992-93 demonstrated a large shift in size frequency of bonefish to smaller size classes in 1992-93 (Figure 4). The abundance of larger individuals was much lower in 1992-93 samples.

Bonefish sampled in fisher landings during 1992-93 had mean length and weight, 35.7 cm and 0.67 kg, respectively (Table 5). The average length of bonefish sampled in fisher landings during 1992-93 was lower than in gill-net samples (Table 5; Fig. 4). Although most fish in fisher landings were not sexed, a very conservative estimate of the percentage of nonreproductive bonefish taken by fishers would be 30% based on the smallest reproductive individual sampled in gill-net samples (male: 32.0 cm).

Results of the bonefish sampling of 100+ individuals greater than 35 cm provided data for additional comparisons. Since the sampling was exclusively for large individuals, larger-sized females should have been overrepresented. For this sample, the sex ratio was 42:67 (female:male), or 0.63:1, which was still biased towards males (Table 6). The mean length of males and females in this sample was 40.1 cm and 44.2 cm, respectively.

Table 5. Bonefish data (mean ± s.d.) from fisheries-independent sampling using gill nets in Tarawa lagoon, 1977 - 1992-93, and from fisheries-dependent sampling of fishers in South Tarawa, 1992-93.

	GILL NET SAMPLING		FISHERMEN LANDINGS
	1977	1992-93	1992-93
TOTAL FISH			
Mean length (cm)	46.4 ±4.1	37.6 ±7.3	35.7 ±6.6
Mean weight (grams)	1313.4 ±317.8	835.2 ±260.3	666.0 ±428.4
Sample size	41	36	1831
Sex ratio (female:male)	17:24 (0.71:1)	4:27 (0.15:1)	
Males			
Mean length (cm)	44.6 ±4.1	37.4 ±7.9	
Mean weight (grams)	1170.4 ±322.1	825.9 ±236.7	
Females			
Mean length (cm)	49.1 ±3.0	37.8 ±6.2	
Mean weight (grams)	1515.3 ±228.1	935.8 ±416.0	
Smallest reproductive size (cm)			
Male	42.5	32.0	
Female	46.5	35.0	

Table 6. Results of bonefish sampling of individuals larger than 35 cm from fisher landings sampling in Tarawa Lagoon, 1992-93.

SEX	NUMBER	LENGTH (cm)	WEIGHT (g)
Male	67	40.1	959.1
std. dev.		4.0	275.0
range		23.4-51.3	500-2250
Female	42	44.2	1232.6
std. dev.		4.9	465.3
range		35.0-55.7	550-3000
SEX RATIO			
female:male	42:67 (0.63:1)		

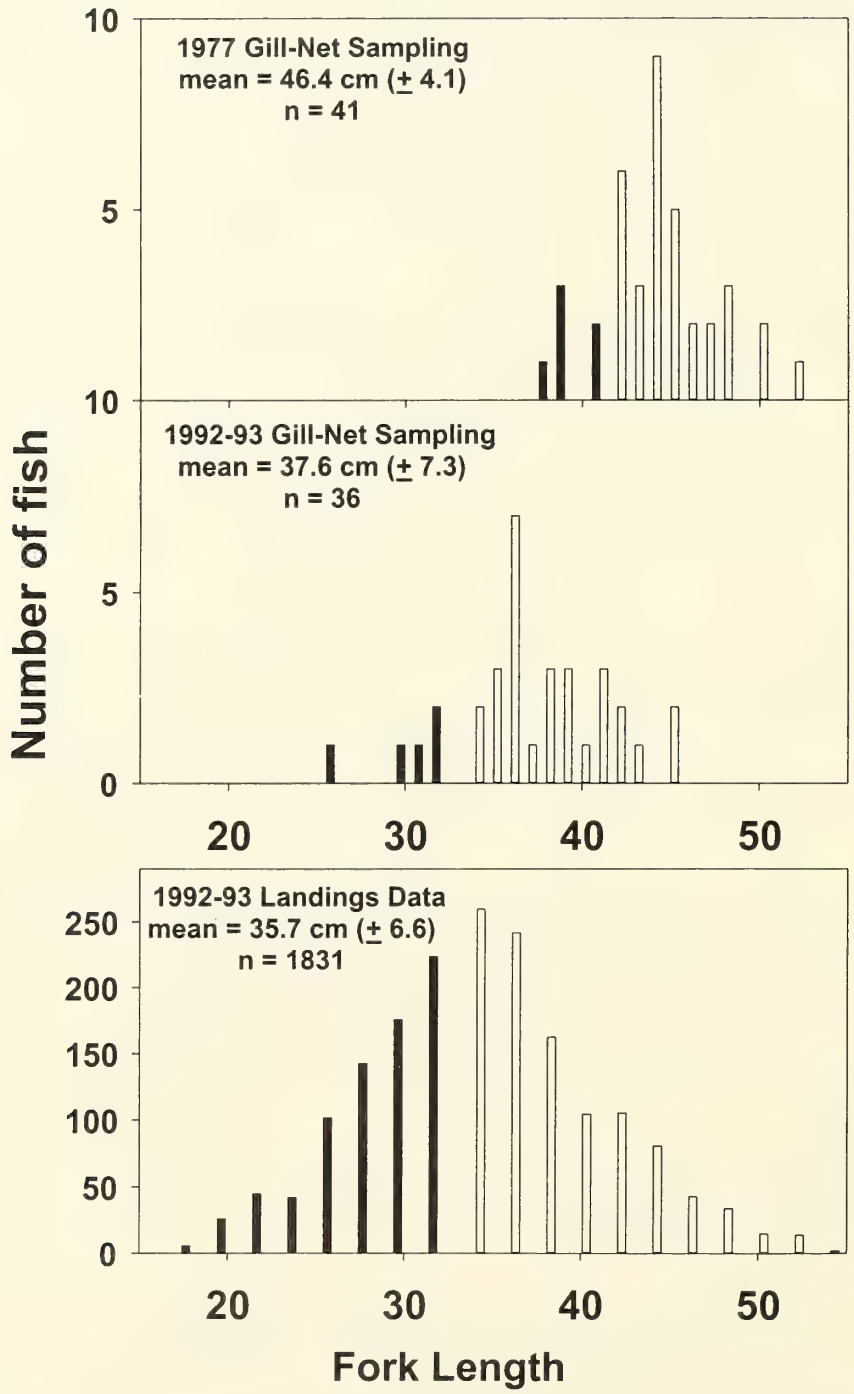

Figure 4. Comparison of length-frequency data for bonefish, *A. glossodonta*, caught during 1977 and 1992-93 gill net sampling and from 1992-93 fisher landings. Dark bars represent immature fishes; open bars represent fishes above size of first reproduction.

DISCUSSION

Review of existing literature and information from this investigation suggest that finfish resources of Tarawa Lagoon continue in a state of decline. Reports completed by the Kiribati Fisheries Division during the past two decades provided information on a declining lagoon fishery (Cross 1978, Marriott 1984, Mees 1987, Mees 1988 a&b, Mees et al. 1988, Wright and Yeeting 1988). Results from this investigation support and extend those conclusions.

Increased fishing pressure in Tarawa Lagoon is a response of increased population growth and the need for more fishery products. Unfortunately, many species in Tarawa Lagoon have experienced declines in abundance at least partially due to increased fishing pressure. Johannes and Yeeting (this volume) have provided important documentation from fishers on declining resources. Several conditions point to the condition of declining stocks. For example, fishers have increased use of the "splash method" of fishing gill nets in the lagoon due to low catch rates with gill nets alone. Such changes in fishing methods signal problems in lagoon fisheries.

Habitat alteration and loss, especially the construction of causeways, has caused a decline in fish migration to spawning sites (see discussion by Johannes and Yeeting, this volume). Channels are vital for the migrations of lagoon species which migrate to offshore sites during their spawning period. Additionally, causeways may block larval fish migration through channels into the lagoon following their early planktonic development offshore. Currents that develop during tidal exchange in the lagoon may provide the necessary cue for migration. Causeway construction obviously has resulted in loss of spawning migrations and may have contributed to declines in abundances of some species, particularly bonefish.

It would appear that the lagoon fishery has become overcapitalized. Considering the finite resources, the increase in use of monofilament gill nets and outboard engines has contributed to the overfished condition. Historically, Kiribati fishers were noted for using many fishing methods for a diversity of species (Kock 1986, Teiwaki 1988). The trend in recent years has been toward use of efficient gear, such as gill nets, and targeting fewer species. Such a trend has the inevitable consequences of declining stocks.

Bonefish (*Albula glossodonta*), the most important fish harvested in Tarawa Lagoon, demonstrated significant declines in CPUE effort and average size (for total individuals and both sexes) based on comparisons of the data from this study and the 1977 study (Cross 1978). Bonefish was the dominant species landed by fishers using gill nets in Tarawa Lagoon during this study. Of great concern is the shift in sex ratio from 0.71:1 (F:M; 1977) to 0.15:1 (1992-3). Shifts in sex ratio may be indicative of stressed populations, although much variability exists among samples, populations, and species, and differences should be cautiously interpreted (Sadovy 1996). Since male bonefish mature at smaller size than females, the intensive fishing effort, especially for larger fish, may have resulted in females being underrepresented in the population. Loss of large females for egg production could result in spawning failure for the population.

Fisher-landings data collected during 1992-93, suggested that a large percentage of bonefish caught in Tarawa Lagoon were prespawning individuals and that females, which have a larger mean size, have been selectively depleted. The conservative estimate of the

number of bonefish landed by fishers that were below reproductive size was 30% (based on the smallest reproductive individual captured during fisheries-independent sampling). Since the greatest proportion of mature fish were males, the spawning stock of females within Tarawa Lagoon was apparently low. These results, in combination with the information obtained on spawning migration failure, indicate a critical condition for bonefish in Tarawa Lagoon with great potential for spawning failure in this species throughout the lagoon (see Johannes and Yeeting, this volume).

Analyses of other species demonstrated similar differences as those observed for bonefish. An example is the spangled emperor (*Lethrinus nebulosus*), which is one of the most preferred lagoon species. This species was much lower in proportion of catch and had lower CPUE in fisheries-independent samples taken in the lagoon in 1992-93 than in 1977. Spangled emperor ranked fourth in abundance in gill-net samples in 1977 but were uncommon in 1992-93 samples.

CPUE in fisheries-independent samples was significantly lower in 1992-93 than in 1977. This suggested that fisher catch rates were lower than in previous years and that increases in the amount of gear and fishing farther from previous fishing areas has been necessary to land the same amount of fish. As habitat is degraded and overfishing increases in areas, fishers are forced to fish more intensively for increasing limited resources in Tarawa Lagoon.

Distribution of catch in fisheries-independent sampling was not even throughout Tarawa Lagoon. Lower CPUE was observed in the southern and eastern portions of Tarawa Lagoon than in other areas for both gill-net and handline sampling. This same trend was documented for coral abundance, whereas deposit-feeding and suspension-feeding invertebrate distribution was reversed (Paulay, this volume). Most lagoon fishes are dependent on coral structure for shelter; therefore, the distribution of coral abundance should be closely correlated with fish abundance. Lower fish abundance in the eastern and southern portions of the lagoon could be influenced by habitat alteration/loss in addition to the intense fishing pressure.

Beach seine sampling demonstrated large changes in fish assemblage structure between the 1977 and 1992-93 studies. Several previously abundant species, primarily baitfishes, were not captured during 1992-93 seine samples. This supports information from fishers who stated that baitfishes have declined dramatically since the Betio-Bairiki causeway was constructed and intensive baitfishing was initiated to support the tuna fleet.

The results of this investigation suggest declining finfish resources in Tarawa Lagoon. Several management strategies should be considered to improve conditions and resources in the lagoon. A combination of strategies ultimately should be adopted to ensure resource maintenance or improvement. Johannes and Yeeting (this volume) recommend the reestablishment of community management (traditional marine tenure) and protection of prespawning aggregations for Tarawa. The central government should adopt strategies which would conserve resources for the entire atoll (and nation). Two management strategies with great potential for long-term benefit are: 1) the establishment of marine reserves; and 2) the protection of spawning (and prespawning) aggregations. Numerous publications provide the theoretical benefits of reserves and closed spawning areas and empirical improvements within them (Bohnsack 1989, 1996, Beets and Friedlander 1999, Johannes et al. 1999). These strategies allow improved population and community structures, increased biomass, and potentially greater reproductive output, which could act

as "sources" for surrounding fishing grounds. Success of these management strategies requires important considerations such as adequate location and size, and fisher compliance. Other available resources, such as tuna, would possibly allow for lower fishing effort on lagoon resources but would require government incentives. Ultimately, management success will be based on resource user and community support, especially in smaller and remote locations.

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ATOLL RESEARCH BULLETIN

NO. 491

GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 1. HABITAT, BEHAVIOR, AND MOVEMENT PATTERNS

BY

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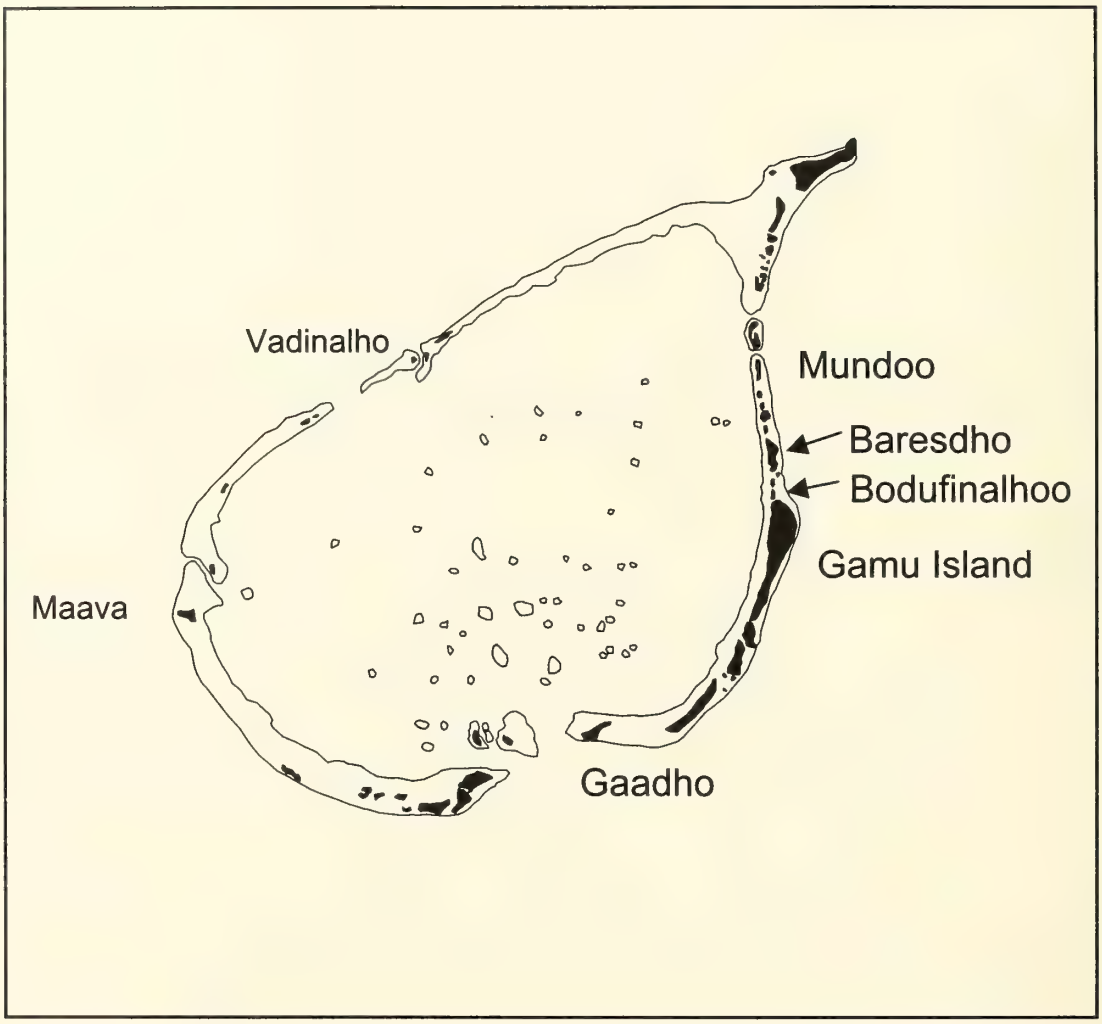

Figure 1. Map of Laamu Atoll showing study sites mentioned in the text.

GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 1. HABITAT, BEHAVIOR, AND MOVEMENT PATTERNS

BY

ROBERT D. SLUKA[1]

ABSTRACT

Grouper and Napoleon wrasse ecology was studied in Laamu Atoll, Republic of Maldives. Studies were divided into three basic categories: 1) habitat utilization; 2) behavior; 3) movement patterns. Habitat use was studied on several spatial scales: 1) among coral reef zones; 2) among sites within a zone; 3) within one site. Behavioral studies focused on how much time grouper spend in cleaning, active, and nonactive behavior. A tagging study was initiated to examine interisland movement patterns. Major results of this study include:

1. Development of a spatial model of grouper-habitat interactions. At the largest spatial scale, grouper relative abundance was predictable among sites of the same habitat type separated by tens of kilometers; several grouper species showed consistent preferences for one type of habitat over another. However, absolute grouper density was not predictable among sites within the same habitat type. Grouper density varied by site and was not significantly correlated with structural features of the surrounding coral reef. At the microhabitat scale, grouper were found more often in areas of a site with specific habitat features.

2. There were species-specific patterns in behavior. Cleaning behavior occupied 0-20% of individuals' time. Active behavior was correlated with size in several species. The amount of time grouper spent being cleaned by cleaner fish differed by habitat type.

3. Smaller grouper species (maximum total length < 50 cm) showed no inter-island movement. In fact, several individuals were observed under the same coral head several months in a row.

4. Grouper density did not vary through time at permanently marked transects. This was due to both the stationary nature of their habits and the high variability in the data.

INTRODUCTION

Groupers (Pisces: Serranidae, subfamily Epinephelinae) are top-level predatory fish found in warm waters throughout the world (Heemstra and Randall, 1993). Of the 15 genera and 159 species known to date, 8 genera and 66 species are found in the western Indian Ocean, Red Sea or Persian Gulf (Heemstra and Randall, 1993). The most abundant genera in this region is *Epinephelus*, constituting 68% of known species.

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Juvenile groupers have a greater spatial distribution than adults (Jory and Iverson, 1989) and tend to live more near-shore (Beaumarriage and Bullock, 1976). This pattern is most likely due to the dispersal of larvae out of the range of environmental conditions in which adults can survive (Jory and Iverson, 1989). Juveniles are cryptic, not straying far from crevices and staying under coral heads (Nagelkerken, 1979a). Gag *Mycteroperca microlepis* and red grouper *Epinephelus morio* juveniles show an ontological shift in habitat, migrating from seagrass beds to reefs as they grow (Ross and Moser, 1995). Eggleston (1995) showed that post-settlement Nassau grouper (25-35 cm total length (TL)) were found exclusively in algal-covered coral clumps, early juveniles (60-150 cm TL) were found outside of, and adjacent to, algal-covered coral clumps, and larger juveniles (> 150 cm TL) were associated with patch reefs.

Juvenile groupers have a greater abundance of crustaceans in their diet than any other taxonomic group. Crabs were the dominant prey item of juveniles on Bahamian patch reefs (Grover et al., 1992). Adult groupers are generalized, opportunistic carnivores exhibiting an ambush mode of feeding, staying close to the substrate, and lunging while expanding their mouth and engulfing their prey (Parrish, 1987). Groupers can also suck prey out of crevices by rapidly expanding their mouths (Burnett-Herkes, 1975). They feed at all times of the day, but feeding tends to be crepuscular, peaking at dusk and dawn (Parrish, 1987; Sluka and Sullivan, 1996a). There is no shift in diet with depth at the taxon level. However, the species composition of prey items changes with depth (Parrish, 1987), probably because of differences in distribution of prey items as opposed to changes in selection by groupers. Prey consumption differs by habitat type, season and grouper size (Harmelin-Vivien and Bouchon, 1976; Kingsford, 1992). It is generally thought that as groupers grow larger their diet shifts from mainly crustacean to mainly fish, but data suggest that prey preferences are species specific.

Grouper tend to be secretive fish, occupying caves, crevices, and ledges (Smith, 1961). Juveniles tend to occur closer to shore than adults (Stewart, 1989). Groupers require habitat for shelter, food, and cleaning stations (Parrish, 1987; Sullivan and de Garine, 1994). The relative abundance of groupers varies among coral reefs at several spatial scales. At the largest spatial scale, there are biogeographic differences in grouper relative abundance. For example, several grouper species are found on coral reefs along the continental shelf regions of the northern Indian Ocean that are not found in the coral atolls of the Maldives (Heemstra and Randall, 1993). Within a biogeographic province, grouper relative abundance differs among coral reef types or zones (Alevizon et al., 1985; Shpigel and Fishelson, 1989; Sluka and Sullivan, 1996b; Sluka and Reichenbach, 1996). These differences among zones may be consistent among biogeographic provinces. For example, *Cephalopholis argus* is most abundant on reef crests in both the Gulf of Aquaba and the Republic of Maldives (Shpigel and Fishelson, 1989; Sluka and Reichenbach, 1996). Several species of grouper are loosely attached to structural features of coral reefs, such as *Plectropomus* spp., *Variola louti*, and *Gracila albomarginata* (Sluka and Reichenbach, 1996).

Red hind *Epinephelus guttatus* home-range size was not related to body size and had a median value of 862 m^2 (Shapiro et al., 1994). Graysby home-range size was estimated as 23.7 m^2 for 5-15 cm individuals and 27.6 m^2 for 15-25 cm individuals (Sullivan and Sluka, 1996). *Cephalopholis argus*, *C. hemistiktos*, and *C. miniata* home range sizes were found up to 2000 m^2, 62 m^2 and 475 m^2 , respectively. Larger grouper

species, such as *Plectropomus leopardus* (maximum total length > 1 m), can have home-range sizes up to 18,797 m^2 (Zeller, 1997). Tagged groupers have been shown to have high-site fidelity and return to their original reefs when displaced (Bardach, 1958). However, a small percentage of individuals may travel long distances to spawning aggregations or simply move over time (Samoilys, 1997).

The demand for fresh seafood by wealthy Asians has fostered a lucrative trade in live reef fish throughout the Indo-Pacific. Reef fish, especially grouper, are caught by fishermen, held in cages, then shipped by boat or air to Hong Kong, China, or Singapore. This fishery has resulted in overfishing in a number of countries and has fostered the use of fishing practices that destroy coral reefs (cyanide and dynamite use). A fishery for live grouper has recently started in Maldives and is now showing signs of overfishing (fish less abundant, smaller in size, fishermen moving farther away from previous fishing grounds to seek more fish). Little is known about the biology and ecology of grouper from Maldives. This study provides basic information on grouper ecology that can be used to develop a management plan for a sustainable live fish-food trade.

This study seeks to add to the basic knowledge of grouper ecology in the Indian Ocean in general and specifically in Maldives. Data were collected in three main areas of study: 1) distribution among habitat types; 2) behavior; 3) movement patterns. This study presents some of the first information on grouper ecology in Maldives.

METHODS

Study site

The Republic of Maldives is a chain of coral reef atolls stretching from about 7 degrees north latitude to 0.5 degrees south latitude. This study was carried out at the research facility of the Oceanographic Society of Maldives located on Gamu Island, Laamu Atoll (Fig. 1). The southern atolls of the Maldives are distinctly different than the northern ones, having fewer channels and consequently, larger, unbroken coral reef structures (Anderson, 1992). For the purposes of this study, reefs have been placed into three main categories: outside atoll rim, inside atoll rim, and faros. Reefs found on the side of the islands facing the open ocean are termed outside and those on the side of the islands facing into the central atoll lagoon are termed inside. Faros are circular reef structures that rise from the central atoll floor. There is a typical zonation for most reefs progressing from inshore to offshore with a shallow sandy lagoon, reef flat, reef crest, and reef slope. The outside atoll rim reef slope drops precipitously to about 30-50 m, slopes gently for about a half kilometer to 125-170 m depth, then drops again to abyssal depths (Anderson et al., 1992; Anderson, 1998). The inside atoll rim reef slope drops steeply to about 20-30 m and then grades into a sandy bottom which occupies the inner portion of the atoll. Laamu Atoll inner lagoon reaches 73 m in depth. Faros are similar in zonation with a reef flat, crest and slope.

Length estimation training

Observers were trained to estimate grouper size accurately to the nearest 5 cm following the method of Bell et al. (1985). Thirty-five pvc lengths were cut to roughly approximate a normal distribution. Pvc pipes were strung along a 3 mm rope and laid in a sandy area of Gamu harbor at approximately 8-10 m depth. Observers slowly swam by

the pvc lengths at a distance of approximately 3 m and recorded the lengths in 5 cm categories on underwater paper (< 7.5 cm, 7.6-12.5 cm, 12.6-17.5 cm, ... 77.5-82.5 cm). Observers then compared their estimate to the true distribution of pvc lengths and determined their particular bias (i.e. under- or over-estimating length). This process was then repeated. On the third pass, the observers were asked to estimate the size of the pvc length and then examine the actual size which was discreetly written on the pipe. Observations are considered accurate to +/- 2.5 cm.

Habitat

An atoll-wide survey was conducted by examining three types of reef slopes (outside atoll rim, inside atoll rim, and faros) each at four sites: Gaadhoo, Maavah, Mundoo, and Vadinalhoo (Fig. 1). At each site, six 15-minute surveys were completed consisting of two observers swimming side by side in a zig-zag pattern between 9 m and 18 m depth. Both observers searched for *Cheilinus undulatus*, *Plectropomus areolatus*, *P. laevis*, *P. pessuliferus*, and *Variola louti*.

The four former species are highly sought after for the live fish-food trade and all five species are amenable to rapid and accurate identification and enumeration using this method (Newman et al., 1997). These species are rarer than smaller grouper species which makes them less amenable to sampling using plot-based survey methodologies (i.e. transects or point counts). The two observers helped each other and all results were recorded on one tally sheet. Groupers within site range were enumerated and their size estimated to the nearest 5 cm. Water visibility was such that the bottom was visible even if deeper than 18 m. All groupers observed were counted even if outside the depth boundaries, which were chosen mainly for diver safety. Data were analyzed using a one-way nested ANOVA with habitat as the fixed factor and sites nested in habitat. Data were tested for homoscedasticity and log(x+1) transformed where appropriate. A presence/absence list of all grouper species observed was compiled while searching for the aforementioned species. Species counts were analyzed using one-way ANOVA with habitat as the main factor in one analysis and east/west sites in another analysis.

Transects (12 m x 20 m, width by visual estimation, n=14) were lain in the inner atoll rim reef slope habitat between Gamu and Bodufinalhoo (Fig. 1) and the total number of *Cephalopholis argus* enumerated. Size of each fish was visually estimated following training (Bell et al., 1985). Size was converted to biomass using a weight-length relationship calculated from unpublished data collected in Maldives (Sluka, unpublished data). Relief of the site was assessed by randomly selecting 10 1-m^2 quadrats along the length of the transect line and measuring the vertical distance between the deepest and shallowest point in the quadrat. A Pearson correlation coefficient was calculated to determine if there was a significant relationship between *C. argus* biomass and vertical relief.

Microhabitat utilized by groupers was compared to the surrounding benthos of the site off the island of Bodufinalhoo (Fig. 1). Six grouper species were observed: *Anyperodon luecogrammicus* (n=4), *Cephalopholis argus* (n=30), *C. leopardus* (n=3), *C. miniata* (n=4), *Epinephelus merra* (n=5), and *Plectropomus areolatus* (n=6). The maximum size of these species ranges from 20-60 cm (Randall, 1992). The point-intercept method was used to assess the benthic composition at the point where a grouper was observed. A 1 m^2 quadrat, divided into 25 points, was lain on the reef and the

benthos under each point was placed into one of ten categories: plate coral, massive coral, branching coral, other coral, macroalgae, octocoral, sponge, sand, rubble or pavement. Pavement was defined as any dead coral surface that was not colonized by benthos, not including turfing algae. Depth was measured from the surface to the midpoint of the quadrat. Relief was calculated as the difference between the shallowest and deepest point in the quadrat. Depth was recorded to the nearest 0.3 m. The general benthos at the site was defined by laying five 50-m transects perpendicular to the prevailing depth gradient. Twenty points along each transect line were randomly chosen to assess the benthos using the same method as above. Due to the reef profile and diving limitations, only 60 quadrats were sampled for the general reef benthos. The mean number of points recorded in each benthos category was compared to the same category for all grouper species combined using a t-test (Zar, 1984). One-way ANOVA was used to compare each benthic category among all grouper species and the general site benthos (Zar, 1984). Post-hoc Tukey tests were used to determine which means were significantly different.

Behavior

The diurnal activity patterns of six grouper species (*Cephalopholis argus, C. miniata, Epinephelus merra, Plectropomus areolatus, P. laevis, P. pessuliferus*) were studied on coral reefs between Gamu and Baresdhoo islands (Fig. 1). Observations occurred January 13-22, 1997 between 1000 and 1400 hours local time. Groupers are known to forage more actively during crepuscular periods (Parrish, 1987; Shpigel and Fishelson, 1989; Brule et al., 1994; Sluka and Sullivan, 1996a). Thus, this study focused on activity patterns and particularly the importance of cleaning behavior during less active times of the day.

Behaviors were defined as one of three categories: cleaning, active, and non-active. A grouper was considered cleaning if a cleaning organism (fish or shrimp) could be observed making contact with the grouper or if a cleaning posture was exhibited (i.e. operculum flared and mouth open). Active behavior was defined as all activities where the grouper was swimming. The majority of observations in this category were from fish only swimming, but rarely included behavior interpreted to be sexual interactions or aggressive intraspecific displays among, presumably, males. Grouper behavior was defined as nonactive when the fish was not swimming, thus remaining stationary at a particular point, on or in, the water column above a coral reef.

An individual grouper was observed for 5-minute periods. The activity of an individual fish was recorded at 20-second intervals. The observation was included in analyses only if a fish was observed for the entire 5-minute period. The size and species of each grouper observed were recorded. Groupers were categorized as small, medium, or large for ANOVA based upon terciles of the maximum length for each species (Table 1).

The data were analyzed separately for cleaning, active, and nonactive behavior due to the lack of independence between observations. Histograms and normal probability plots were examined to determine if data were highly nonnormal (Zar, 1984). The cleaning data were judged to be too skewed to use parametric ANOVA (102 of 143 observations were recorded as 0). Nonparametric Kruskall-Wallis ANOVA was used to analyze cleaning behavior data. Additionally, observations on each grouper species were placed into one of two categories: cleaning or not cleaning, regardless of how much time.

Table 1. Size values used for classifying grouper into small (S), medium (M), and large (L) categories. Maximum values taken from Randall (1992).

Species	S (cm)	M (cm)	L (cm)	Max. size (cm)
Cephalopholis argus	<15	16-30	>30	50
C. miniata	<15	16-25	>25	41
Epinephelus merra	<10	11-20	>20	28
Plectropomus areolatus	<20	21-40	>40	60
P. laevis	<35	36-65	>65	100
P. pessuliferus	<25	26-50	>50	70

a species actually spent cleaning. A Chi-square contingency table was used to assess the independence of species and cleaning behavior. Cleaning observations for *C. argus* were placed in these same two categories as well as separated by size category: small, medium or large. All other species had too few observations to warrant a separate analysis by size using Chi-square (Zar, 1984).

A two-way ANOVA was used to analyze active and nonactive behavior with species and size as fixed factors for each of the three behavior categories. Residual plots were examined for homogeneity of variance and data log(x+1) transformed were appropriate (Zar, 1984). As two species were lacking one of the size categories (*E. merra* and *P. pessuliferus*), there were only four species compared by ANOVA. Size was never significant as a factor in the ANOVA (see results). This factor was then dropped from the model so that all six species could be included in a one-way ANOVA with species as the fixed factor and the number of 20-second time intervals observed at a particular activity the replicates. A post-hoc Tukey test was used to determine which species had significantly different means. Variances remained heterogeneous after transformation for nonactive behavior, thus nonparametric Kruskal-Wallis ANOVA was used to assess differences among species for this activity category. A Pearson correlation coefficient was used to examine significant relationships between species and size for each activity separate from ANOVA.

Tagging study

Grouper were collected using hooks and lines between November, 1996 and February, 1997. Snorkelers baited hooks with damselfish or fusiliers which were dangled in front of individual grouper. This method appears to work well with *Aethaloperca rogaa*, *Cephalopholis* spp. , and *Plectropomus* spp. In order to catch *Epinephelus fuscoguttatus* and *E. polyphekadion*, tuna heads were used as bait on hooks and lines from a boat at night, especially in the channels leading outside the atoll. Each fish was brought back to the boat, measured for fork length (mm), placed in a preweighed bucket and weighed (g). A dart tag, with a alphanumeric plastic piece attached on the end was inserted into the dorsal musculature so that the tag secured itself under the pterigiophores of the dorsal fin. Air was released from the swim bladder when expansion was observed. Fish under 250 mm were deemed too small for tagging due to the size of the tag. *Epinephelus fuscoguttatus*, *E. polyphekadion*, and *Plectropomus* spp. were double tagged, with one tag placed on each side of the fish in the same position as described above.

Permanent transect sampling

Three 240-m^2 transects were established at each of two sites on the inner atoll reef slope off Bodufinalhoo Island (Fig. 1). The boundaries of each transect were marked with flagging tape and small subsurface buoys which floated approximately 1-2 m off the bottom. Two transects at each site were at approximately 10 m depth while the third ranged from 10-20 m depth. Each month one observer surveyed the transect and recorded the species and size of each individual observed. This data was then plotted by month for all sites combined to examine the variability in grouper density and species composition through time. A repeated-measures ANOVA was used to test for significant differences in mean grouper density (no. 240 m^{-2}) among grouper species, between the two buoy sites, and among repeated sampling dates.

RESULTS

Habitat

The abundance of *Cheilinus undulatus*, *Plectropomus pessuliferus*, and *Variola louti* was significantly different among habitat types (faros, inside and outside the atoll), but not significantly different for *P. laevis* or *P. pessuliferus* (Table 2). The site-nested-in habitat factor was significant for all species except *P. areolata*. *Plectropomus pessuliferus* was most abundant in faros, and least abundant outside the atoll (Fig. 2). *Variola louti* was most abundant outside the atoll, while least abundant inside the atoll.

No Napoleon wrasse were observed in quantitative surveys in inner atoll rim or faro reef slopes (Fig. 2). Abundance of Napoleon wrasse was significantly higher in the outer-atoll rim than the other two habitat types. There was significant variance in the abundance of Napoleon wrasse among outer-atoll rim-reef slope sites.

Twenty grouper species were observed during the 15-minute surveys and a total of 25 during the course of the entire study (Table 3). There were no significant differences in the total number of grouper species observed among habitat types ($F=0.128$, $p>0.05$). However, there were significantly more species observed on the eastern side of the atoll than on the western side ($F=7.096$, $p<0.05$).

Table 2. Summary of ANOVA results comparing mean grouper abundance among habitat types (inside atoll rim, outside atoll rim and faro reef slopes) and sites (n=4 per habitat)—nested-within-habitat types. Probability levels for each factor are given.

Species	Habitat factor	Site (Habitat) factor
Cheilinus undulatus	<0.001	<0.001
Plectropomus areolatus	NS	NS
P. laevis	NS	NS
P. pessuliferus	<0.001	<0.05
Variola louti	<0.001	<0.05

There were significant differences between the general-site benthos and all grouper-combined benthos for the categories of relief ($t=-4.506$, $df=110$, $p<0.001$), massive coral cover ($t=-3.335$, $df=110$, $p<0.001$), algae cover ($t=-2.148$, $df=110$, $p<0.05$) and sand cover ($t=3.786$, $df=110$, $p<0.001$). All other benthic categories showed no

significant differences. Grouper were found more often at points on the coral reef with higher relief, more massive corals, greater algal cover and less sand (Fig. 3).

There were significant differences among the general-site benthos and grouper-species benthos for the benthic categories of relief ($F=5.066$, $p<<0.001$), massive coral ($F=6.986$, $p<<0.001$), and sand ($F=2.723$, $p<<0.05$). *C. argus* (Fig. 4) and *C. miniata* were found more often in areas of higher vertical relief than were the surrounding benthos. *C. argus* was also found more often in areas of greater massive coral cover than the surrounding benthos (Fig. 4). *C. leopardus* was found more often in areas of greater massive coral cover than the surrounding benthos and all other grouper species, including *C. argus*. The surrounding benthos had a greater percentage of sand cover than positions where *C. argus* were found (Fig. 4)

Table 3. Checklist of grouper species observed during this study. See text for habitat definitions.

Species	Outside	Inside	Faro	Lagoon
Anyperodon luecogrammicus	+	+	+	
Aethaloperca rogaa	+	+	+	
Cephalopholis argus	+	+	+	+
C. boenak		+		
C. leopardus	+	+	+	
C. miniata	+	+	+	
C. sexmaculata		+	+	
C. spiloparaea		+	+	
C. urodeta	+	+	+	
Epinephelus caeruleopunctatus	+	+	+	+
E. fasciatus	+	+		
E. fuscoguttatus	+	+	+	
E. macrospilos		+		
E. melanostigma	+	+		
E. merra		+	+	+
E. ongus		+		
E. polyphekadion	+	+	+	
E. spilotoceps	+	+		
E. tauvina	+	+		
Gracila albomarginata	+	+	+	
Plectropomus areolatus	+	+	+	
P. laevis	+	+	+	
P. pessuliferus	+	+	+	
Variola albimarginata	+			
V. louti	+	+	+	

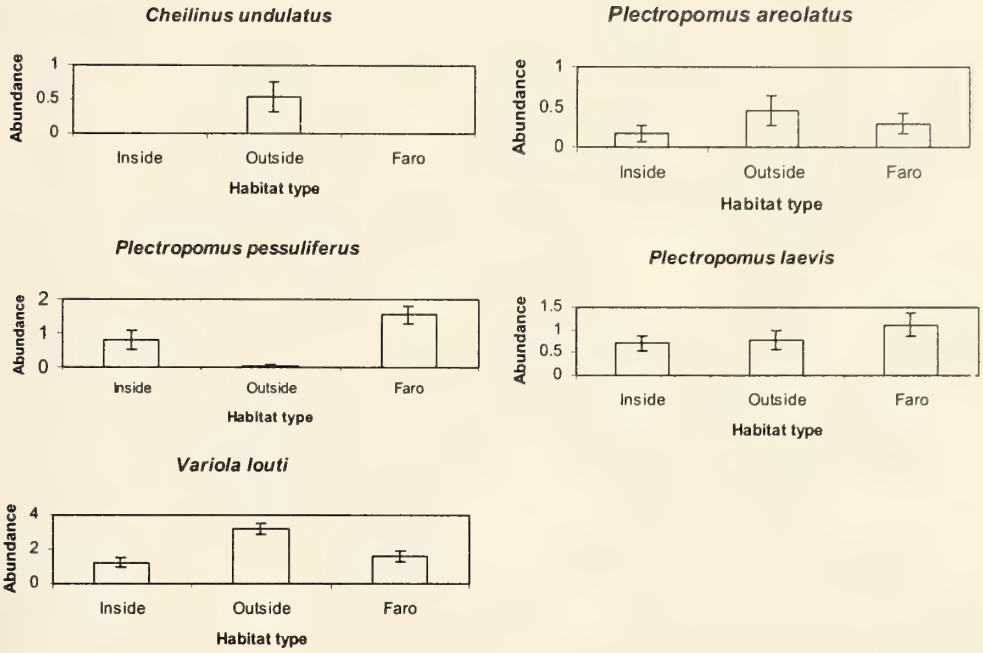


Figure 2. Mean abundance (no 15 minute $^{-1}$) among three reef slope habitat types: inside the atoll rim, outside the atoll rim, and in faroes.

Behavior

One hundred forty three grouper were observed among six species: *Cephalopholis argus* (n=75), *C. miniata* (n=19), *Epinephelus merra* (n=15), *Plectropomus areolata* (n=13), *P. laevis* (n=14), and *P. pessuliferus* (n=7). There were significant differences in the mean time spent cleaning among the six grouper species ($p<0.05$, Figure 5). *E. merra* was never observed cleaning. There is high variability in the data with *P. laevis* observed to spend the most time cleaning (approximately 20%). The amount of time spent cleaning was significantly related to size in *C. argus* ($r=0.23$, $p<0.05$), but in no other species.

Cleaning behavior was independent of species ($X^2=8.85$, df=5, $p>0.05$). The distribution of number of groupers observed cleaning is similar to those observed not cleaning, except for the case of *E. merra*. Cleaning behavior and size were independent for *C. argus* ($X^2.091$, df=2, $p>0.05$).

Neither size, species, nor the interaction effect were significantly influencing the amount of time spent on active behavior by observed groupers ($p>0.05$). Size was dropped from the model and all six grouper species were examined for significant differences in active behavior (see methods). There were significant differences in the amount of time spent in active behavior among species ($p<0.001$). Figure 5 and a Tukey test showed that *E. merra* spent significantly less time in active behavior than the other species. There were no significant differences among all other species. Size was significantly correlated with active behavior in *C. miniata* and *P. pessuliferus* (Fig. 6).

There were no significant differences in nonactive behavior among species, size categories, nor in their interaction ($p>0.05$). There were significant differences among species when size was dropped from the model and all six species included ($P<0.001$).

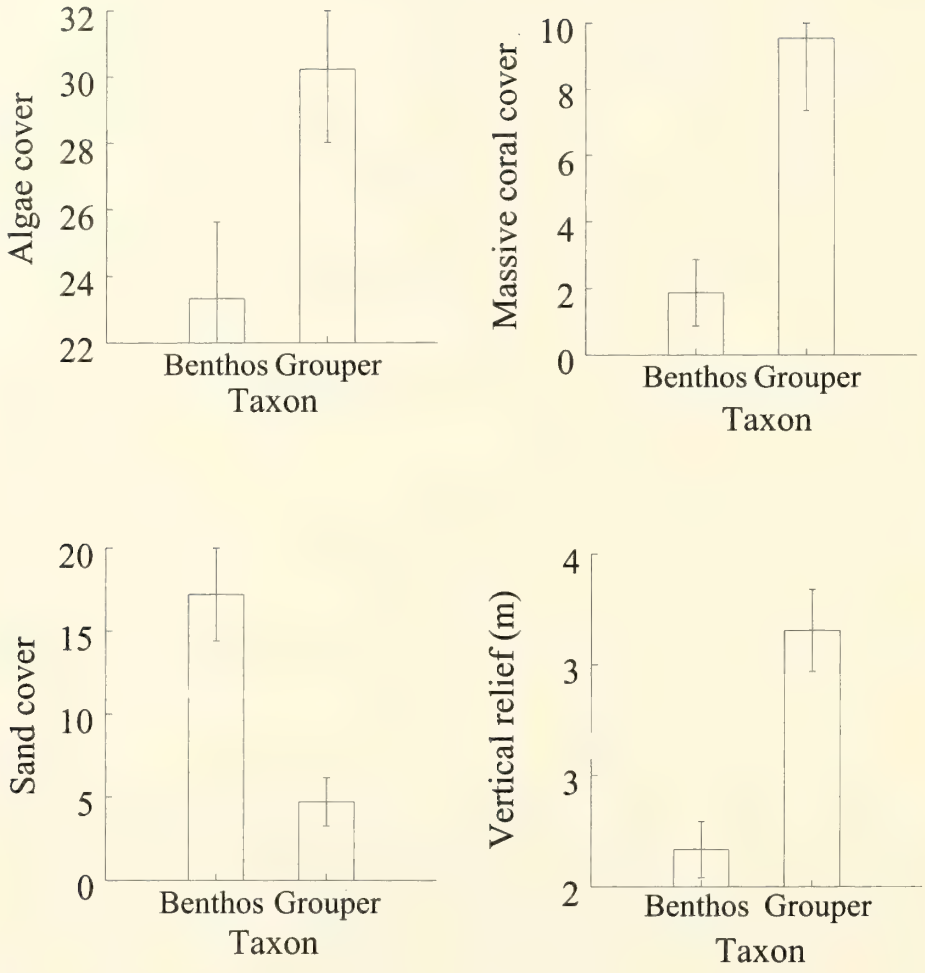


Figure 3. Plots showing differences in the habitat use by grouper versus the general surrounding benthos of the site. Histogram bars for each taxon show the value of the habitat variable (relief or percent coverage) where 52 individual groupers were observed and 60 1 m^2 plots of the surrounding coral reef.

Figure 5 shows that *E. merra* spent significantly more time in nonactive behavior than all other species. Figure 6 shows that there were significant relationships between *C. miniata* size and the amount of time spent on nonactive behavior. Larger individuals spent less time on nonactive behavior than smaller individuals. The relationship between time spent on nonactive behavior and size for *P. pessuliferus* was almost insignificant ($p=0.055$).

Tagging study

Two hundred four grouper among nineteen species were caught during the tagging study. Sixty-two percent (127/204) of these individuals were of a taggable size. The most frequently caught species was *Cephalopholis argus*, followed by *Epinephelus*

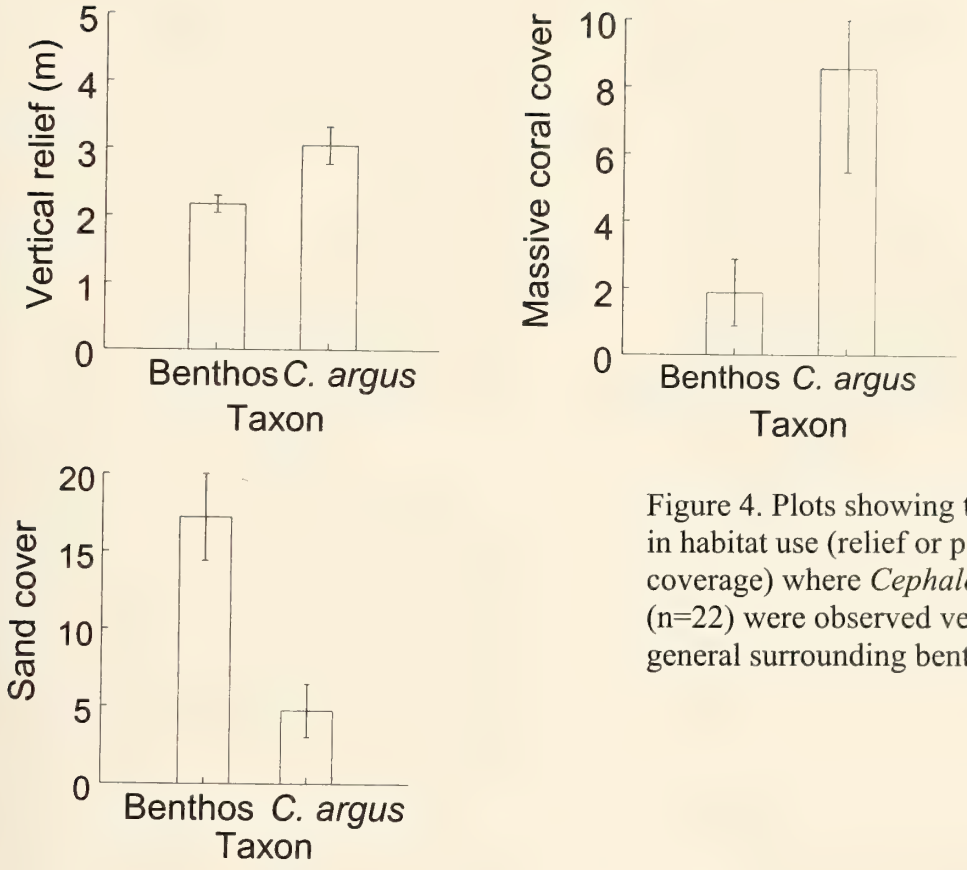


Figure 4. Plots showing the differences in habitat use (relief or percent coverage) where *Cephalopholis argus* (n=22) were observed versus the general surrounding benthos (n=60).

spilotoceps and *C. miniata*. None of these species are targeted in the live fish-food trade, but appear to be most easily caught. The targeted species, *E. fuscoguttatus*, *E. polyphekadion*, and *Plectropomus* spp., constituted only 13% of grouper caught during the tagging study. The tag return rate was about 9%, as 11 tags were returned or sighted underwater. Five of these 11 tags could not be used to provide information on movement patterns due to the tag being unreadable underwater, problems with fishermen reporting returns, or fish purposely being displaced to examine homing behavior. Of the six fish for which there is reliable data, three (two *C. argus* (287 and 355 mm TL) and one *Aethaloperca rogaa* (360 mm TL)) were observed at the same site 183, 145, and 145 days later, respectively. One of these two *C. argus* was observed at the permanent transect site repeatedly, almost always in the same 240 m^2 transect. The *A. rogaa* was resighted twice underwater, one month apart, both times under the exact same coral head. There was also no interisland movement for one *C. miniata* (320 mm TL, 18 days between captures), one *Gracila albomarginata* (314 mm TL, 57 days), and one *P. laevis* (366 mm TL, 19 days).

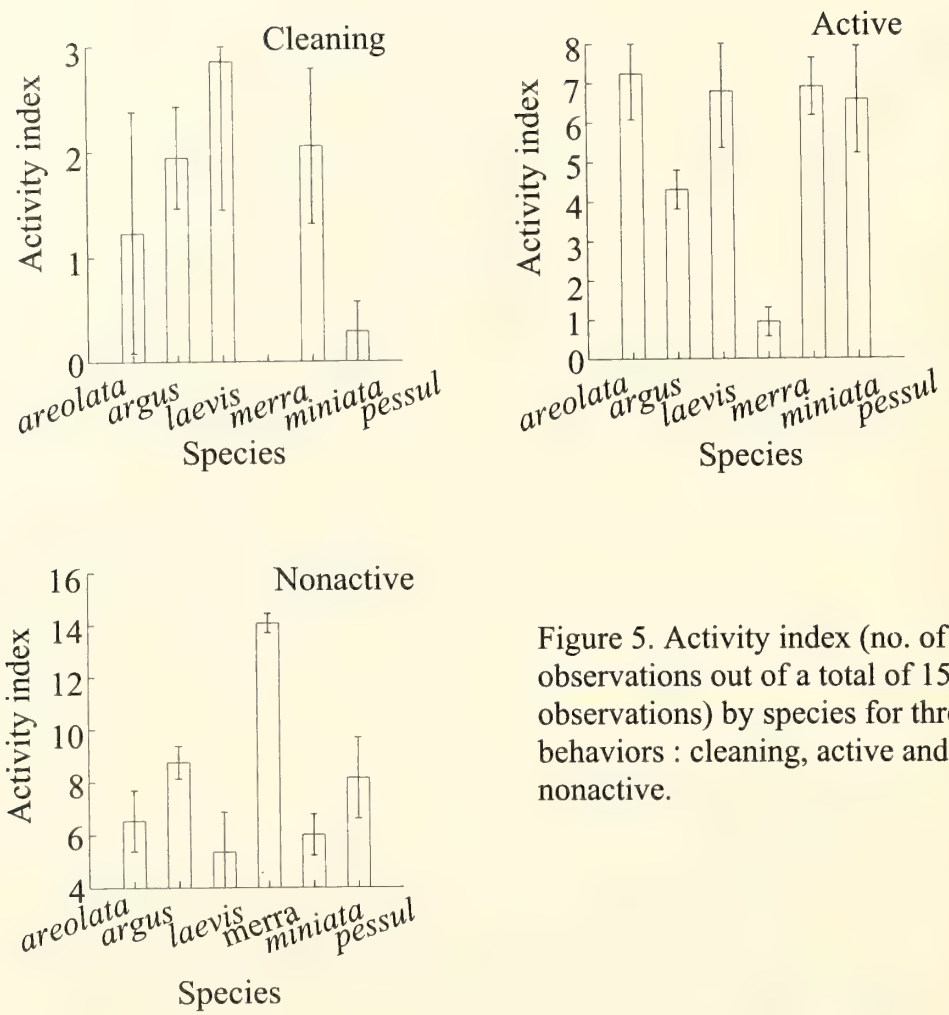


Figure 5. Activity index (no. of observations out of a total of 15 observations) by species for three behaviors : cleaning, active and nonactive.

Permanent transect sampling

There were significant differences in mean grouper density among species. A post-hoc Tukey test indicated that there were significant differences in species density for each of the nine time periods when considered separately. *Cephalopholis argus* density was greater than *C. miniata* density and both were greater than all other grouper densities (Figure 7). There was no significant difference in grouper density between the two buoys and no species x buoy factor interaction. This indicates that the overall grouper density was not significantly different between the two buoys and that no species was significantly more abundant at one buoy or the other. There was also no significant difference in overall grouper density through time, nor any interaction factor between time and grouper species or site. This indicates that grouper density did not change significantly through time nor did it change through time for any species. The change in *C. argus* density through time was examined separately, but was also not significantly

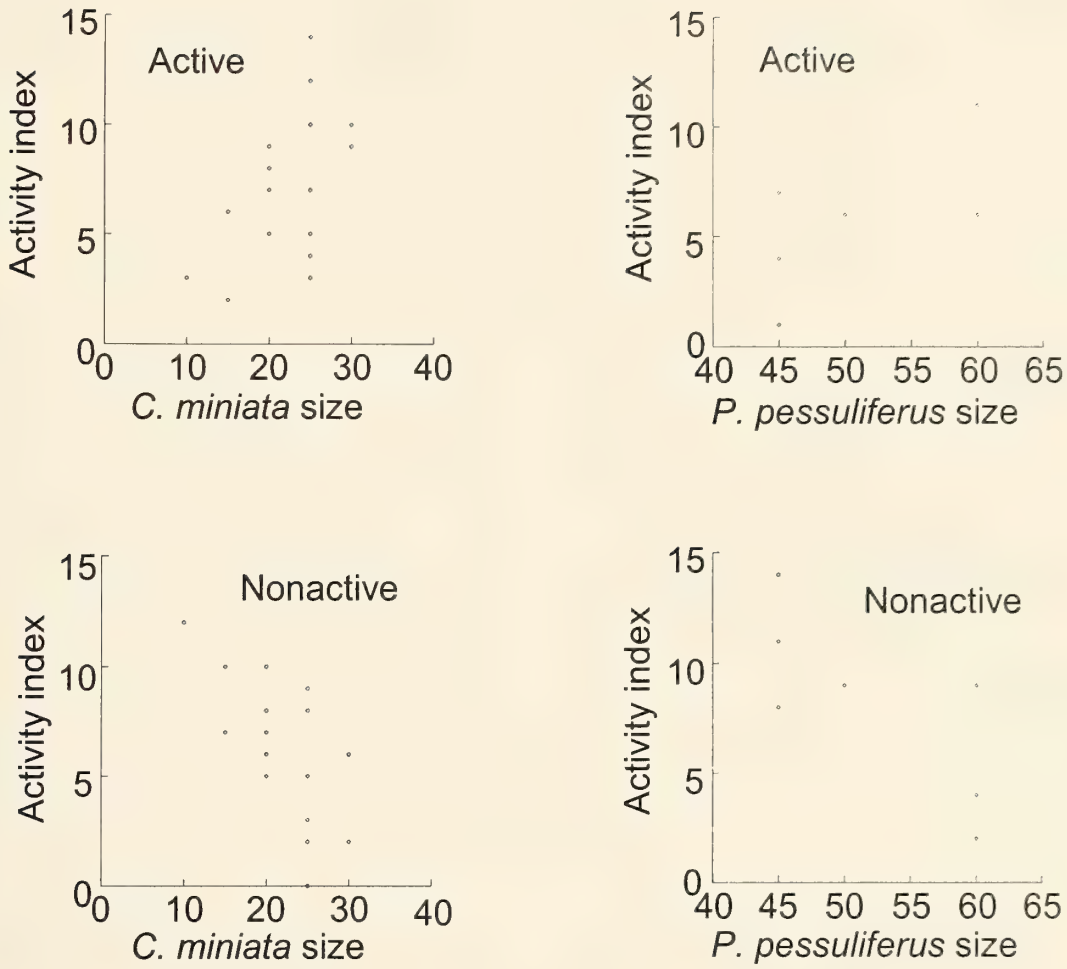


Figure 6. Relationship between active and nonactive behavior indices and grouper size. As the activity index increases, the amount of time an individual spent at a particular behavior increases.

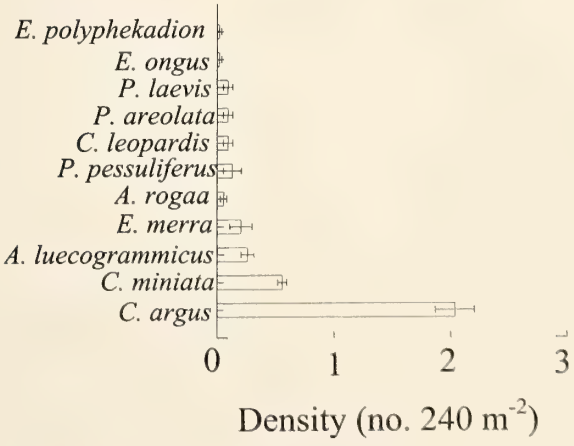
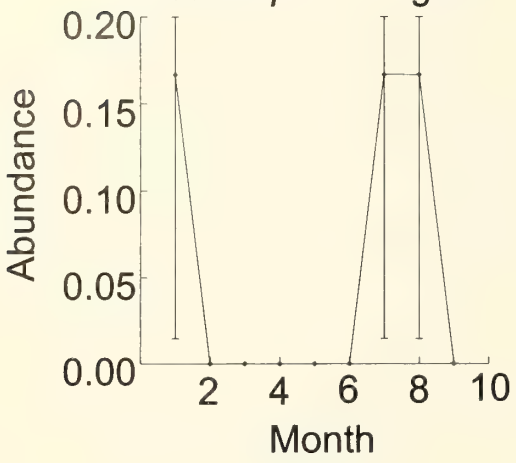
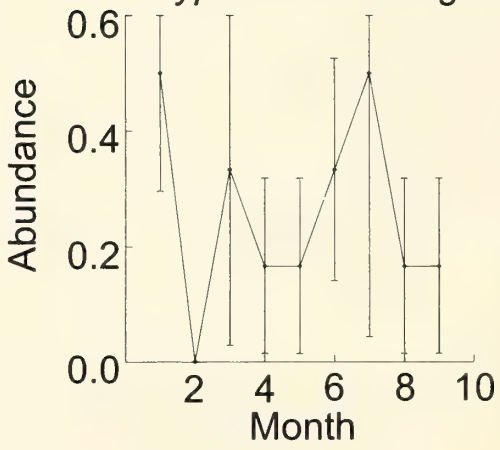


Figure 7. Grouper density in permanent transects.

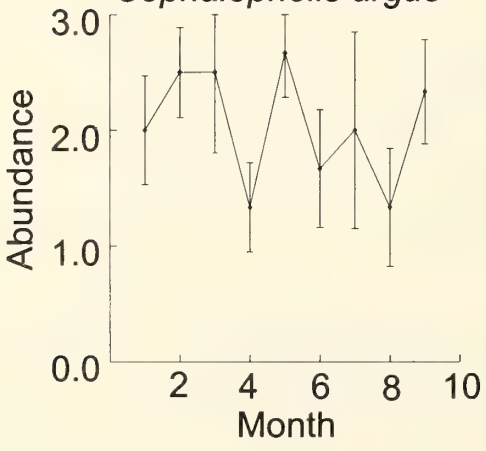
Aetheloperca rogaa



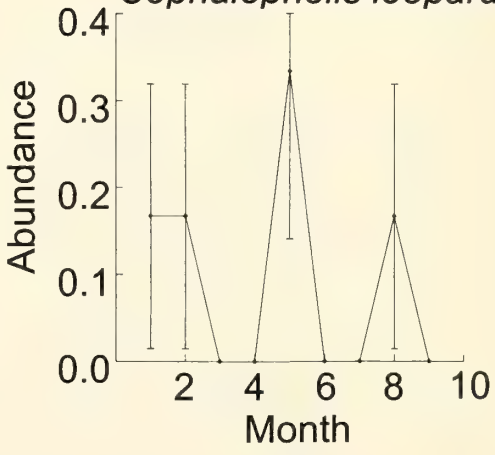
Anyperodon luecogrammicus



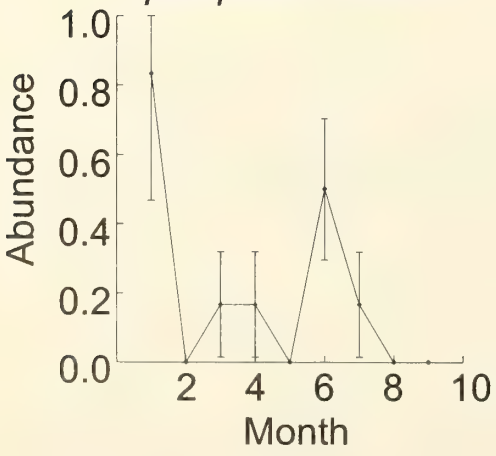
Cephalopholis argus



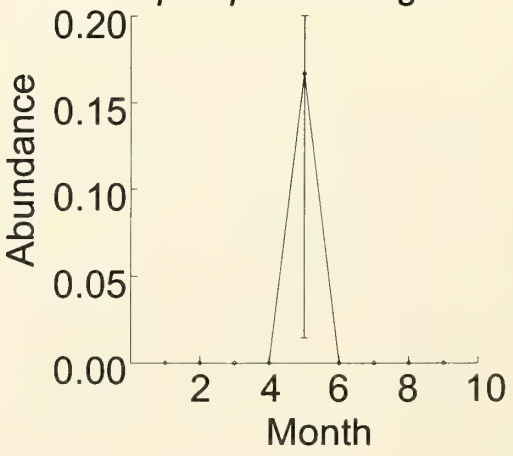
Cephalopholis leopardus



Epinephelus merra



Epinephelus ongus



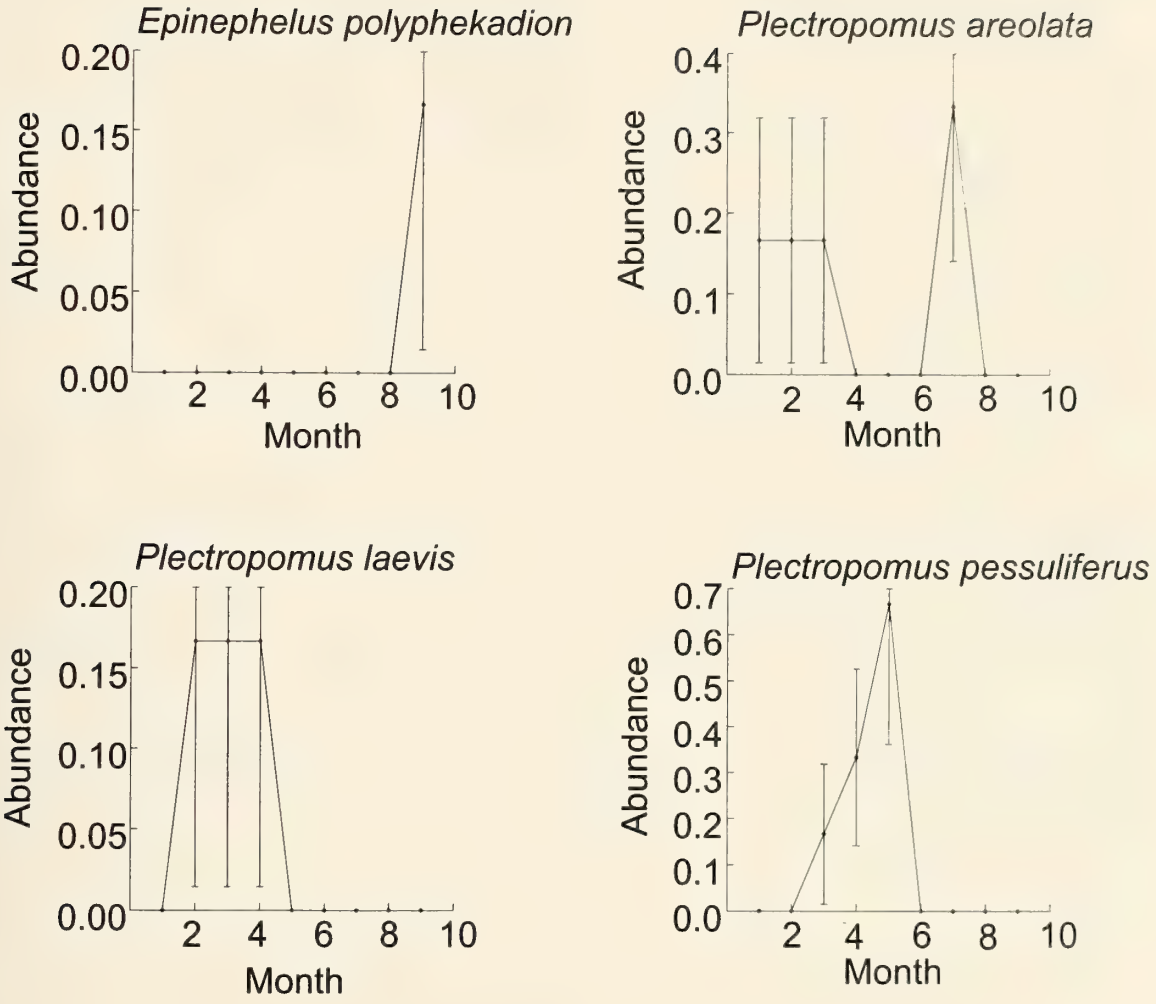


Figure 8. Mean abundance (no. 240 m^{-2}) in six permanent transects. Months start in November 1996 (1) and end in July 1997 (9).

different ($p>0.05$). Figure 8 shows that there was significant variance among monthly means

DISCUSSION

Habitat

Many coral-reef fish species and assemblages are known to be qualitatively and/or quantitatively related to particular features of the reef structure. Families such as the Labridae, Chaetodontidae, and Scaridae are only found in coral-reef habitats (Choat and Bellwood, 1991). Quantitative features of the reefs themselves, such as coral cover or habitat complexity, influence the relative abundance of species and absolute abundance of particular species (reviewed in Jones, 1991). The relationship between habitat and coral-reef fish abundance varies depending upon the scale one examines.

Relationships between quantitative features found at a microscale do not necessarily hold between reefs separated by many meters or kilometers (Syms, 1995).

The relative abundance of grouper varies among coral reefs at several spatial scales. At the largest spatial scale are biogeographic differences. For example, several species of grouper are found on coral reefs along the continental shelf of the northern Indian Ocean that are not found in Maldivian atolls (Heemstra and Randall, 1993). Within a biogeographic province, the relative abundance of grouper differs among coral-reef types or zones (Alevizon et al., 1985; Shpigel and Fishelson, 1989; Sluka and Sullivan, 1996b; Sluka and Reichenbach, 1996; Newman et al., 1997). These differences may be consistent among biogeographic provinces. For example, *Cephalopholis argus* is most abundant on reef crests in both the Gulf of Aquaba and the Republic of Maldives (Shpigel and Fishelson, 1989; Sluka and Reichenbach, 1996). Quantitative relationships between absolute abundance and habitat parameters have been few. Nagelkerken (1979b) showed a significant relationship between coral cover and graysby (*C. cruentata*) abundance. Sluka et al. (1996a) showed a similar relationship for this species in the central Bahamas, but not in the Florida Keys (Sluka, 1995). It appears that fishing has a much greater influence on the abundance of grouper species that are targeted by fisheries than on quantifiable habitat features (Sluka et al, 1996b, 1997). On the smallest spatial scale, the behavior of groupers has been shown to be significantly influenced by the surrounding habitat (Sluka, 1995; Sluka et al, in press). Groupers were found to spend more time in microhabitats of coral reefs with specific habitat features (e.g. cleaning stations, high vertical relief). Sluka (1995) found that *C. cruentata* preferentially occupied high-relief habitats over surrounding low-relief habitats and that larger fish were found more often in microhabitats of higher relief than smaller fish. Similarly, Sluka et al. (1998) found that the average size of *C. cruentata* was greater in higher-relief coral-reef types than lower-relief types.

Grouper habitat relationships in Maldives

Two grouper species were more abundant in a particular habitat than others. This likely indicates a preference for these habitats rather than the result of fishing as fishing pressure has been low. *Variola louti* was most abundant on reef slopes outside the atoll rim while *Plectropomus pessuliferus* was most abundant in faro reef slopes. Randall and Brock (1960) stated that *V. louti* was most abundant in passes between islands and on the outside of the barrier reef in French Polynesia. *Epinephelus merra* was the dominant grouper in lagoonal Acroporid patch reefs. This is consistent with other studies showing this species to be abundant in shallow water lagoons (Randall and Brock ,1960; Chave and Eckert, 1974; Heemstra and Randall, 1993; Sluka and Reichenbach, 1996). There were significant differences in density among sites for most species indicating that, while there may be general preferences for one habitat type over another, a species' absolute abundance cannot be predicted by knowledge of habitat type. This is consistent with grouper habitat studies in the Caribbean (Sluka, 1995; Sluka et al., 1996b) and Australia (Newman et al., 1997).

Sluka and Reichenbach (1996) studied the density of groupers among several types of habitats in Gaagandu, North Male Atoll and Olhugiri, Thaa Atoll. The median number of groupers 240 m^{-2} on an inner-reef slope was much greater than on reef crests or a large Acroporid reef. Twenty-two species of grouper were observed, with *C. miniata*

and *C. urodeta* being the most abundant on the reef slope, *C. argus* on reef crests and the Acroporid reef. *Epinephelus merra* was the most abundant grouper in shallow lagoons. At Thaa Atoll, Sluka and Reichenbach (1996) surveyed both the outer- and inner-reef crest grouper assemblages. The outer- and inner-reef crests were both dominated by *C. argus*. However, *C. urodeta* was more abundant on the outer-reef crest. In Laamu Atoll, *C. urodeta* are more abundant on outer-reef slopes than inner-reef slopes.

Diversity did not differ significantly among the three reef-slope habitats in this study. However, diversity was greatly reduced in lagoonal habitats. There were 25 species observed throughout the course of this study, but only 3 in lagoons. Shakeel and Ahmed (1996), Adam et al. (1998), and Anderson et al. (1998) list 41 species as occurring in Maldives. Several species were observed on reefs inside the atoll rim and on faros, but not outside the atoll rim: *Cephalopholis sexmaculata*, *C. spiloparaea*, and *Epinephelus merra*. Only one species, *Variola albimarginata,* was observed outside the atoll rim, but not in other habitats. However, only one individual of this species was observed during the course of this study.

Groupers were shown to have specific microhabitats that were utilized preferentially to the surrounding habitat. Fish were found more often in areas of higher structural complexity. This was evidenced by individuals being located in areas of higher vertical relief, greater massive coral (likely also reflecting relief) and algal cover, and lower sand cover. This corroborates the general observation that groupers prefer caves, crevices and holes (Smith, 1961).

While groupers behaviorally prefer areas of a coral reef with high relief, knowledge of this habitat feature cannot be used to make predictions about grouper abundance. Thus, while grouper relative abundance on a large scale (biogeographically and among types/zones of coral reefs) has predictability, the abundance at a particular site appears to be influenced more by factors such as recruitment variability and fishing pressure than habitat. This is especially true for species targeted for harvesting. Some smaller species in the Caribbean have shown quantitative relationships between habitat features and abundance (Nagelkerken, 1979a; Sluka et al., 1996a). This was not the case for the abundant grouper *Cephalopholis argus* in Maldives.

Sluka and Reichenbach (1996) also made observations on the degree of association between grouper and their habitat. Several grouper species such as *Plectropomus* spp., *Variola louti*, and *Gracila albomarginata* were loosely attached to structural features of coral reefs. *Aethaloperca rogaa* appeared to be intermediate between these free-roaming species and the more site-attached species such as *Cephalopholis* spp. and *Epinephelus* spp. Several *Cephalopholis* species had significantly clumped distributions likely indicating the patchy nature of their habitat and the close association with habitat features. In this study, *C. argus* was found more often in sites with a higher vertical relief, greater massive coral cover, and lower sand cover. This is similar to many grouper species that prefer areas with high vertical relief (Nagelkerken, 1979a; Sluka et al., 1996a). This result indicates that *C. argus* will be found more often within a particular site where there are specific habitat features of the coral reef. Can *C. argus* abundance then be predicted among sites based on these same features? Based on these observations and those of other grouper species in the Caribbean (Sluka, 1995; Sluka et al., 1996a,b, 1998, in press) and Australia (Zeller, 1997), it appears that the movement patterns and behavior of grouper within a coral reef are affected

significantly by specific, quantifiable features of the coral-reef habitat. The most likely position of a grouper on a particular coral reef can be predicted based upon a knowledge of habitat preferences of the grouper and quantified habitat features of the coral reef. However, this knowledge will not allow one to predict the abundance of grouper across a wide spatial scale (i.e., among coral reefs). Knowledge of the habitat features of a coral reef does not generally correlate with the abundance of individuals.

Behavior

Grouper behavior studies have mainly focused on spawning activities (e.g. Smith, 1972; Shapiro, 1987; Carter, 1988; Donaldson, 1989, 1995a; Samoilys and Squire, 1994; Zabala et al., 1997), with the exception of a few studies examining time-activity budgets (Sullivan, 1993; Sullivan and de Garine-Wichatitsky, 1994; Donaldson, 1995b; Sluka and Sullivan, 1996a), diel behavioral changes (Collette and Talbot, 1972; Nemtzov et al., 1993) and inter- and intra-specific interactions (Shpigel and Fishelson, 1991; Donaldson, 1995b). Diel, seasonal and habitat-related differences in predation were studied by Kingsford (1992) and Brule et al. (1994).

Groupers are active throughout the day with crepuscular peaks of foraging activity (Parrish, 1987; Sluka and Sullivan, 1996a; but see Brule et al., 1994). There appears to be little activity at night (Zeller, 1997); however, some species will feed during the night (Randall, 1965, Brule et al., 1994; Sluka, pers. obs.). Grouper spend a significant portion of their day resting, usually perched on a coral head or perhaps hiding in and amongst the numerous holes on a coral reef (Donaldson, 1995b; Sluka and Sullivan, 1996a). Behavior patterns are influenced by the disruption of social structures (e.g. fishing) (Sullivan, 1993). There also appear to be some weak differences in behavior between males and females (Donaldson,1995b). Grouper activities and behavior are significantly influenced by cleaning activities (Sluka and Sullivan, 1996a; Sluka et al., 1999).

The cleaning of ectoparasites by conspecifics has been attributed either to a mutually beneficial relationship in which both host and cleaner receive benefits (Poulin and Vickery, 1995) or a parasitic relationship in which hosts are stimulated into behavioral changes which allow cleaners to feed easily (Losey, 1993). There is little evidence that the lack of ectoparasite cleaning affects fish health (Youngbluth, 1968; Losey, 1972; Gorlick et al., 1987; Grutter, 1996a; Poulin and Grutter, 1996). However, fish spend significant amounts of time cleaning (Poulin and Grutter, 1996; Sluka and Sullivan, 1996a) and cleaners can remove great amounts of parasites (Grutter, 1996b). Grouper may spend significant amounts of time being cleaned (Sluka and Sullivan, 1996a; Samoilys, 1997) and space utilization is directly influenced by the presence or absence of a cleaning station (Sluka et al., 1999). It appears that the proximate cause of cleaning behavior, from the fishes' point of view, is tactile stimulation (Losey, 1993). From the cleaner's perspective, feeding appears to be the motivation for cleaning behavior (Poulin and Grutter, 1996).

In this study, cleaning behavior differed among species from the small grouper species *Epinephelus merra,* which was never observed cleaning, to the large grouper species *Plectropomus laevis* observed cleaning approximately 20% of observation time. There was, though, no general relationship between size and the amount of time spent cleaning as might be expected due to higher parasite loads on larger individuals. Sluka et

al. (1999) hypothesized that cleaning stations may also be used in dominance hierarchies to show the dominant individual. They came to this conclusion after observing the largest grouper in the experiment displace smaller grouper and other species (including a much larger barracuda) from the cleaning station and then move on and not be cleaned. This behavior was also observed one time in this study where a larger *Cephalopholis argus* individual displaced a smaller individual of this species from a cleaning station. The coral grouper *C. miniata* was observed cleaning about 13% of the observation time. However, Figure 9 shows that when the actual time spent cleaning is not considered, more individuals were observed to clean during an observation time than not clean. This species tends to move a lot, having one of the highest indices of active behavior. Thus it appears that this species cleans often, but not for long durations.

Active behavior, defined as a behavior involving swimming, was significantly less in *Epinephelus merra* than in other species. Two species, *Cephalopholis miniata* and *Plectropomus pessuliferus*, showed increasing active behavior with increasing size. Thus, larger individuals spend more time swimming, presumably foraging and potentially engaging in reproductive behavior. Shpigel and Fishelson (1989) showed that the home-range size of males and the larger individuals is greater than females.

Tagging study

The general conclusion of the tagging study is that smaller grouper species generally do not move significant distances during a six-month time scale. In fact, one individual was observed underneath the same coral head several months in a row. Another individual was almost always observed in the same permanent transect. As will be described more fully in the next section, several non-tagged *C. miniata* were also observed hiding in the same group of coral heads over a nine-month period.

The movement patterns of grouper have been relatively little studied (Zeller 1997). Bardach (1958) showed that grouper stayed at the point of tagging for about one month and then shifted habitat. However, Zeller (1997) showed that grouper did not move significantly over a one-year period. Davies (1995) showed that 74% of recaptured *Plectropomus leopardus* (n=143) were caught in the same 2-2.5 km section of a reef in which they were originally released. Most of the movements of this species were only 200-400 m in distance. However, Zeller (1997) using ultrasonic tagging, showed that daily movements of *P. leopardus* may be up to 835 m (mean of 192 m). The home-range size was up to 18,800 m^2. There was a significant difference in the home-range size between fringing reefs (10,500 m^2) and patch reefs (18,800 m^2). Generally, it appears that most individuals move a very short distance over several months or years, but a few individuals move many kilometers (PDT, 1990; Davies, 1995;Collins et al., 1996). These long-distance movements may be associated with movement to spawning aggregations (Burnett-Herkes, 1975; Van Sant et al., 1994).

Permanent transect sampling

Cephalopholis argus was the most abundant grouper in the six permanent transects. This species did not exhibit significant differences in mean density over time. However, there was significant variability in the data. It is possible that the sample size was too low to detect changes. However, Figure 16 shows that the density range for this species was about one individual per transect. The other species were generally rare and

the density did not change through time as it was generally very low. One transect showed an interesting pattern. In this transect there were large coral heads with several *C. miniata* using them for shelter. This species was only observed in this transect and always underneath these coral heads. The number of fish in the transect ranged from three to five, likely due to the cryptic nature of the habitat rather than new individuals arriving. The fish were noticeably bigger at the end of the study than in the beginning. Data from the permanent transects indicate that the grouper assemblage at this site is variable but relatively stable over the short term.

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ATOLL RESEARCH BULLETIN

NO. 492

GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 2. TIMING, LOCATION, AND CHARACTERISTICS OF SPAWNING AGGREGATIONS

BY

ROBERT D. SLUKA

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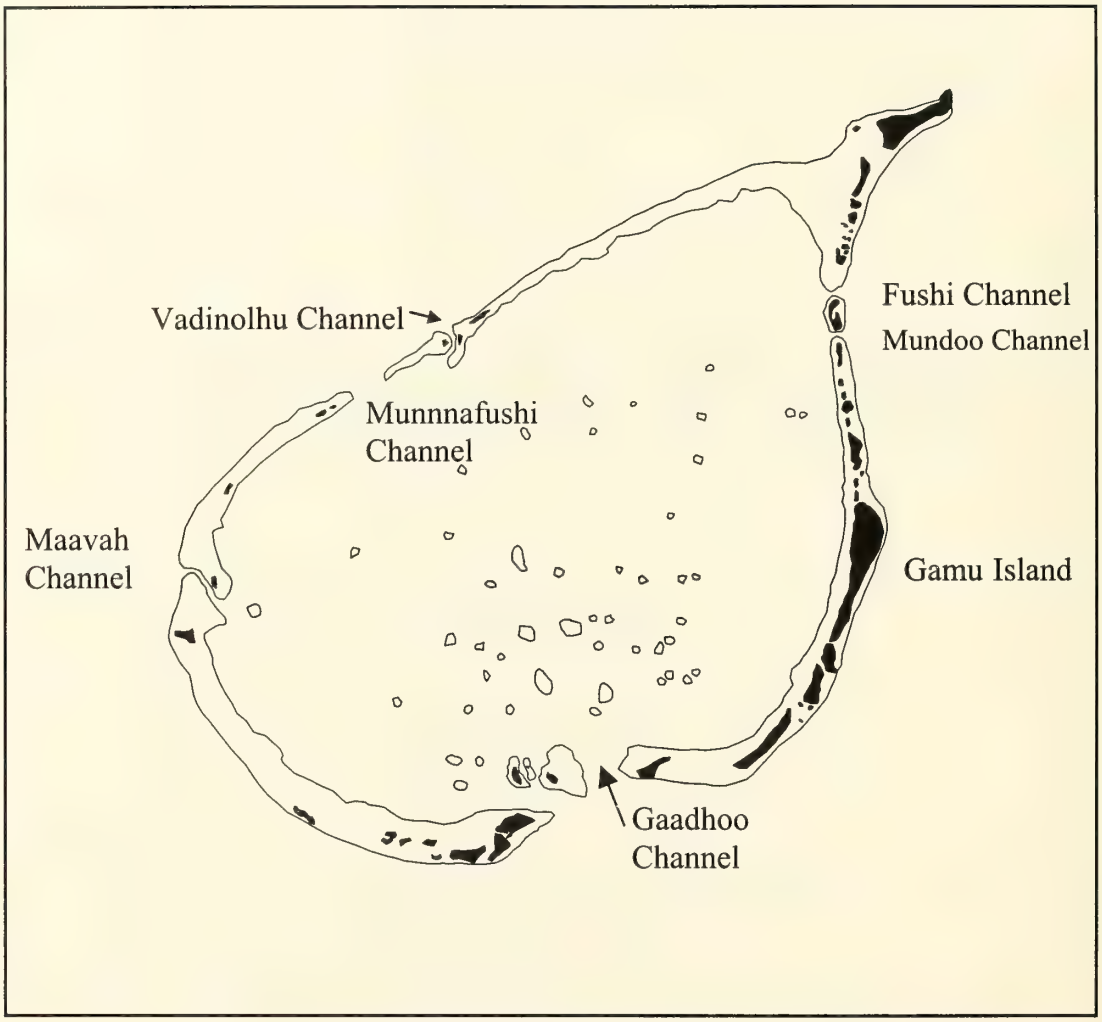

Figure 1. Laamu Atoll, Republic of Maldives. Study sites were located in the channels connecting the inner-atoll lagoon to the open ocean. Black indicates land and gray indicates coral reef or shallow-water lagoonal habitats.

GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 2. TIMING, LOCATION, AND CHARACTERISTICS OF SPAWNING AGGREGATIONS

BY

ROBERT D. SLUKA[1]

ABSTRACT

The reproductive ecology of five species of grouper and the Napoleon wrasse was studied March-June, 1998 in Laamu Atoll, Republic of Maldives. Research focused on identifying the timing, location, and characteristics of spawning aggregations in this atoll.

Timed surveys were used to assess fish abundance and size distribution in Mundoo Channel, which is one of seven channels connecting Laamu Atoll's inner atoll lagoon to the open ocean. Through a pilot study, and later confirmed in the main study, it was concluded that observations could be conducted and compared over different times of the day, tidal cycles, current speeds, and among observers.

A spawning aggregation of *Plectropomus areolatus*, defined as a three-fold abundance increase over ambient levels, was recorded in Mundoo Channel during the new moon in April, 1998. Data collected during the pilot study suggested that an aggregation occurred in this channel during March, 1998. Courtship behavior for this species was recorded during these two months. Data suggested that *P. laevis* spawned during this time period as well. Spawning was never observed, but abundance increases and courtship behavior indicate that spawning occurred during this time.

INTRODUCTION

The demand for live reef fish by southeast Asian markets has resulted in intense fishing pressure on coral-reef fish resources throughout the Indo-Pacific region. In many countries these resources are now fully- or over-exploited (Johannes, 1997). The main coral-reef fish in demand are the Napoleon wrasse (*Cheilinus undulatus*) and groupers (*Epinephelus* spp. and *Plectropomus* spp.).

The Republic of Maldives is a nation of some 1200 coralline islands stretched across the central Indian Ocean. The main fishery in the Maldives has traditionally been, and still is, for tuna. However, in recent years, coral-reef-based export markets have developed so much that many fishers are turning to more profitable fisheries such as beche-de-mer, giant clam, shark, and most recently grouper. Intense fishing for sea cucumber and giant clam resulted in an almost total depletion of commercially important species prompting banning of giant clam export and regulations on the beche-de-mer fishery (Maniku, 1994). Recently, the Maldivian government has banned shark fishing in 11 atolls where tourist resorts are located (Haveeru, Maldivian newspaper, 1998). This was due to complaints from the tourist industry about the reduction in shark numbers and

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its potential effect on diving tourism. Currently there are no regulations on the grouper fishery and it is showing signs of local overexploitation. Export of Napoleon wrasse is currently banned due to their high value to local and expatriate recreational divers.

Sound biological information on the ecology of targeted species in the live fish food trade is needed to develop sound management. The reproductive ecology of these species is poorly known, yet this knowledge is essential for effectively implementing such management measures as spawning season or area closures and marine fishery reserves (Johannes, 1997). While export of Napoleon wrasse is already banned in Maldives due to the urging of several conservation-minded groups, almost nothing is known about this species' reproductive patterns.

This report focuses on the reproductive ecology of the Napoleon wrasse and several grouper species exported in the live fish food industry. The goal of this research was to identify the timing and location of spawning aggregation sites in one atoll in the south of the Maldives.

METHODS

Study area

Laamu Atoll is located at approximately 2N latitude 73.5E longitude (Fig. 1). There are seven channels in this atoll that connect the inner atoll lagoon to the open ocean. Much of this study focused on Mundoo channel, located on the eastern side of this atoll. This was mainly due to its proximity to the Oceanographic Society's laboratory which is located at the northern tip of Gamu Island. The channels range in depth from approximately 10 m (Munnafushi) to over 50 m (Gaadhoo). Most channels have high coral cover on the sides and front (defined as the edge of the channel mouth emptying into the open ocean). The centers of the channels were usually devoid of any structure and showed scarring due to strong currents. Two of the western channels (Vadinolhu and Maavah) were narrow and had large, high-relief coral spurs running along the middle. In between these spurs was sand or exposed limestone. Mundoo channel, the site where most of this study occurred, was 20 m deep at the center with steeply sloping channel walls. The front of the channel emptied into open ocean over a sill that sloped steeply to about 50 m. At that depth, the slope became less pronounced for about 0.5 km, after which it dropped steeply to abyssal depths (Anderson, 1992).

Pilot study

This study focused on five grouper species (*Epinephelus fuscoguttatus*, *E. polyphekadion*, *Plectropomus areolatus*, *P. laevis*, and *P. pessuliferus*) and the Napoleon wrasse (*Cheilinus undulatus*). Factors that could affect grouper and Napoleon wrasse abundance in channel surveys include: time of day, current speed, tidal cycle, and observers. A pilot study was conducted to examine the influence of these variables on the accuracy and precision of fish-abundance estimates. Timed surveys were used to assess abundance instead of transect lines due to strong currents in the channel. Timed surveys have been used in numerous fish surveys and have been shown to be a reliable and repeatable method for accurately and precisely assessing abundance (Russ, 1984a,b, Newman et al., 1997). Other studies of Indo-Pacific groupers, as well as anecdotal accounts in Maldives, suggest that grouper gather to spawn a few days before the new

moon and that the aggregation quickly dissipates on, or soon after, the new moon (Johannes et al., 1994, Samoilys and Squire, 1994). Based upon previous research and anecdotal reports by fishermen, grouper were expected to spawn in the channels connecting the inside of the atoll with the open ocean. From March 23-28, 1998, five of the seven channels in Laamu atoll were visited using scuba and snorkeling in order to gain an understanding of their layout and to determine how best to survey for grouper and Napoleon wrasse. Grouper habitat mainly occupied the channel sides and front, while the middle and inner atoll edge were mainly barren. It was decided to focus surveys on the front edge and sides of the channels.

The optimal duration for each survey was examined on March 30, 1998. Ten 20-minute surveys were completed by three scuba divers with observers searching five meters on each side for a total transect width of 10 m (during this length of time the entire length of the study channel could be surveyed). During the 20-minute surveys, observers counted and estimated the size of each target species. Observers were trained to estimate fish length and transect width using methods detailed in Sluka (2001). The number of minutes into the dive when the individual was observed was also recorded. The cumulative frequency of all species observed was graphed by time of observation in order to determine if there was some asymptotic value; thereafter few individuals were observed. The relationship between time and cumulative frequency was linear, with no asymptote (Fig. 2). The total number of fish of targeted species observed per 20-minute survey ranged from 2-8, except for one survey during which 23 were observed. This survey was dropped from the analysis as an outlier, but could be indicative of an aggregation occurring during this time. There was a significant relationship between time surveyed and total abundance (all species combined). The relationship was linear and can be described by the following equation: abundance = 0.23*time + 0.55 (df=18, $R^2 = 0.99$). As there was a significant linear relationship between abundance and time, the choice of survey duration was arbitrary. It was then decided to use 10 minutes as the survey length in order to have sufficient replication for accurate and precise estimates.

The influence of time of day, tidal cycle, current speed, and observer on grouper abundance was examined March 31-April 2, 1998. Six to nine surveys were completed three times a day: a.m. (0900-1200), midday (1201-1500), and p.m. (1501-1800). The direction of current flow (flood, slack, or ebb), current speed, and observer were noted for each survey. A one-way ANOVA was used to determine if mean abundance of all species combined and each species separately was significantly different among current directions. Due to prevailing wind patterns, sample size was highly skewed towards flood tide. A two-way ANOVA was then used to assess differences in mean abundance by time of day and observer. There was no significant effect of tidal cycle, time of day or observer on the results. Thus, results could be compared from surveys at different times of the day and on different tidal cycles using several observers. Current speed was measured using a hand-held General Oceanics current meter. The relationship between current speed and fish abundance was tested using a Pearson correlation coefficient (n=38). Values of the coefficient among species ranged from –0.12 to 0.18 and were always highly insignificant indicating that surveys could be compared over a wide range of current speeds.

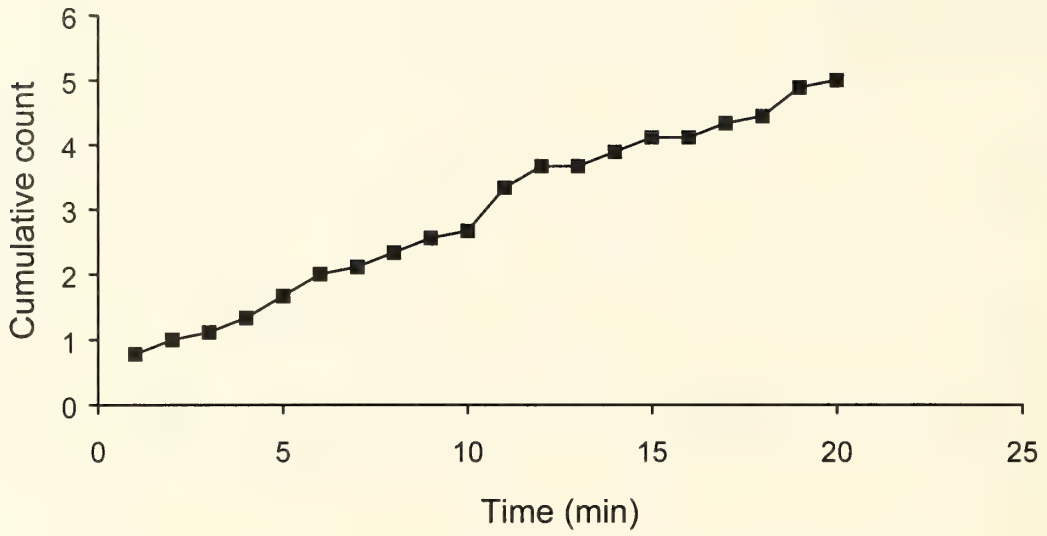

Figure 2. Cumulative count of all target species by total search time.

A spawning aggregation has been defined in the recent literature as an abundance of individuals three times greater than ambient levels (Samoilys, 1997). Using this definition, I calculated the number of replicate surveys necessary to differentiate statistically a three-fold change in abundance, given the variability recorded (Zar, 1984). It was determined that eighteen, 10-minute surveys needed to be completed in each channel to be able to differentiate statistically a three-fold change in abundance using a t-test.

Sampling in Mundoo Channel

Mundoo channel was sampled on nine separate occasions, generally spaced one week apart. The intent was to sample the channel during each of the following lunar phases: new moon, first-quarter moon, full moon, and third-quarter moon. A sampling date fell into a particular lunar category if the sampling occurred three days before or after the calendar date for that period. For example, a new moon occurred on April 25. Sampling occurring April 22-28 was labeled as occurring during a new-moon period. Each sampling event consisted of eighteen, 10-minute surveys: six along the wall nearest Mundoo Island, six along the wall nearest Maabaidhoo Island, and six along the front edge of the channel (nearest the open ocean). Two observers using scuba gear entered the water and surveyed two separate, parallel transects at the same time. There was a distance of at least 10 m separating the two observers, and usually more. If a fish traveled through both transects, it was only counted once, and by the first person who observed it. The size of each fish observed was estimated to the nearest 5 cm.

Even though the pilot study indicated no significant effect of observer, tidal state, lunar period, and date on fish abundance, these factors were more closely analyzed to detect any longer-term effects. Ideally, the data collected could be analyzed as repeated measures, three-factor ANOVA with observer, tidal state, and lunar period as fixed factors, and the repeated measure dated. However, there was unequal replication among

all fixed factors with several categories having only one or no observations. Thus, several separate analyses were made to determine which factors were significantly influencing fish abundance. Data were log(x+1) transformed to help achieve homogeneous variances and normality (Zar, 1984).

A one-way ANOVA was used to test whether or not there were significant differences in the mean abundance (no. fish 10-minute^{-1}) of each fish species among tidal states (ebb, flood, or slack tide). A two-way ANOVA was used to test for significant differences in mean fish abundance among lunar periods and observers. As Mundoo channel was sampled repeatedly, the sampling date was examined in a repeated measures model. The model examined whether or not there were significant differences in abundance among the four species or among dates. Two time periods (April 30 and June 8) had missing values which were substituted with the average value for that time period. The size of each grouper observed was estimated and recorded. A one-way ANOVA was used to test for significant differences in mean fish size among sampling dates.

RESULTS

The total numbers of fish observed in Mundoo channel during the course of this study were: *Cheilinus undulates,* 46; *Epinephelus fuscoguttatus,* 31; *E. polyphekadion,* 7; *Plectropomus areolatus,* 295; *P. laevis,* 96; and *P. pessuliferus,* 12. As this channel was sampled repeatedly, many fish were likely observed several times both within the same sampling date and among sampling dates. Due to low numbers of observations, *P. pessuliferus* and *E. polyphekadion* were not used in statistical analyses.

There was no significant influence of tidal state on fish abundance (Table 1). One-way ANOVA results were always insignificant ($n=175$, $df=2,172$, $p>0.05$). There was no significant difference in *C. undulatus*, *P. laevis*, or *E. fuscoguttatus* abundance among lunar periods or observers (Table 1). There were also no significant interaction effects for these species. *P. areolatus* abundance was significantly different among lunar periods, but not among observers. This species was more abundant in the time period surrounding the new moon than the first-quarter or full moon (Fig. 3). There was no significant difference in mean abundance between the new moon and third-quarter moon lunar periods. Fish abundance was significantly different among species and dates. *Plectropomus areolatus* was the most abundant species during the study, followed by *P. laevis*. The only species which appears to have a recognizable pattern in abundance over time is *P. areolatus* (Fig. 4). It appears that abundance increased during the study until the time period on, and after, the new moon on April 25th. After this date, abundance decreased.

Size-frequency distributions for each species are given in Figure 5. The data conform to known maximum size limits for these species (Randall 1992). Small individuals (<30 cm) were rare. The test showed that there were significant differences in mean fish size among sampling dates only for *P. areolatus* (Fig. 6).

New moons occurred on March 28, April 26, and May 25. Courtship behavior was recorded for *P. areolatus* one and four days prior to the new moon in April. Courtship occurred in pairs, with the larger, presumably male, fish approaching from behind. When the two fish were side by side, the male would turn his body laterally so that he was at a 45-90 degree angle to the female. This placed his vent near the lateral

and ventral side of the female. He then made a shivering motion which consisted of an exaggerated, sustained wave proceeding along the length of his entire body. Once he was ahead of the female, the male would swim directly in front of the female so that the length of his body would pass closely to the female's head region. The larger individual would sometimes shiver in front of the female as well. During most of the courtship displays by *P. areolatus*, the larger individual was dark in color while the smaller was a lighter color. Many of the dark individuals had light bars on the side of their bodies.

Plectropomus laevis usually was not observed in groups but as solitary individuals. However, just after the new moon in March and just before the new moon in April, a small group of 4 to 5 individuals was observed. The largest individual in the group, presumably the male, was 10-20 cm larger than the others. This individual was also colored differently; it was dark with white coloration on the head and tail. Courtship behavior was observed for *Plectropomus laevis* four days following the new moon in March.

No spawning was observed by either species despite several observations at dusk. Once the sun set, individuals retreated to crevices and holes in the coral reef and were not observed swimming out in the open.

Table 1. Summary of Analysis of Variance (ANOVA) results. Tidal state refers to results of a one-way ANOVA testing for significant differences in a species' abundance among periods with ebb, flood, or slack tide. Lunar period refers to results of a two-way ANOVA testing for significant differences in a species' abundance among new, first-quarter, full, and third-quarter moon periods. Observer refers to results of a two-way ANOVA testing for significant differences in a species' abundance among three observers. Ns = not significant, *** = $p < 0.001$.

Species	Tidal state	Lunar period	Observer
Cheilinus undulatus	Ns	Ns	Ns
Epinephelus fuscoguttatus	Ns	Ns	Ns
Plectropomus areolatus	Ns	***	Ns
P. laevis	Ns	Ns	Ns

DISCUSSION

It appears that *P. areolatus* and *P. laevis* spawn near the new moon in March and April in Laamu Atoll, Republic of Maldives. Release of gametes was not observed, but spawning courtship was observed during those times. No courtship behavior was recorded during non-new moon times or during observations near the new moon in May. Based upon abundance data, the major spawning month for *P. areolatus* is April, with minor spawning in March. Formal surveys were not completed in March, but a large number of *P. areolatus* were observed during one portion of the pilot study which occurred two days after the new moon during this month. This timing corresponds with the monsoonal transition from the NE to the SW monsoon. Surveys only spanned the period of March-June, so conclusions cannot be made about other times of the year.

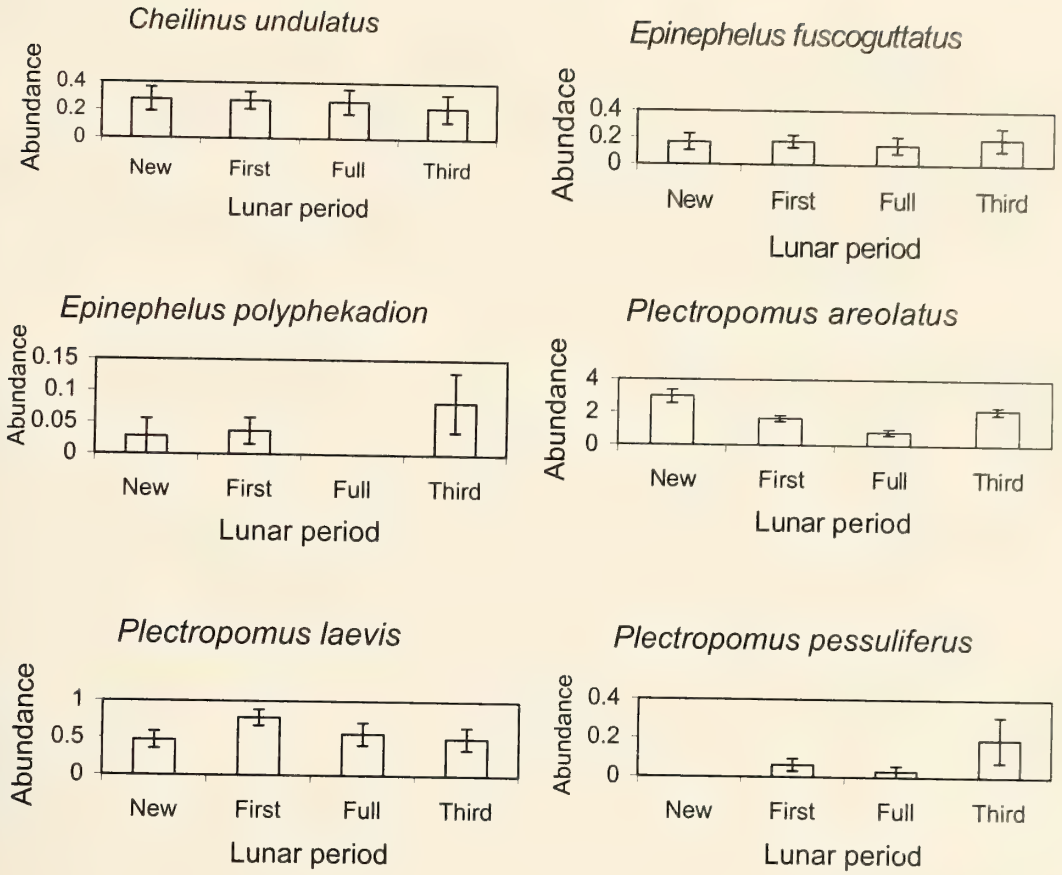

Figure 3. Mean abundance +/- 1 SE (no. fish 10-min^{-1}) of each targeted species in Mundoo Channel by lunar period.

However, spawning may occur during the other monsoonal shift occurring September-October. There is limited evidence that bimonsoonal spawning occurs for some species and locations in the Western Indian Ocean (Morgans, 1962; Nzioka, 1979; Ntiba and Jaccarini, 1990), but other evidence suggests otherwise (McClanahan, 1988).

Courtship behavior of *P. areoloatus* was similar to that of *P. leopardus* observed on the Great Barrier Reef, Australia by Samoilys and Squire (1994). They observed that *P. leopardus* courtship behavior "...involved a specific courtship display whereby the male swam towards a female with his body tilted at 45-90 degrees, quivering along his full length, and making repeated lateral shakes of the head. Continuing in this mode, the male would approach the female and then pass close by the female's head or body, with either the dorsal or ventral side of his body nearest to the female. He would frequently circle and repeat the process." This species pair spawned. Courtship behavior and timing of spawning (new moon, near dusk) may be similar for all Plectropomids.

Both the pilot and main studies indicate that grouper abundance surveys can be undertaken and compared over different times of the day, tidal cycles, current speeds, and among separate observers. Sluka et al. (1994) and Sullivan and Sluka (1996) have also shown that multiple observers and time of day, respectively, do not influence the ability

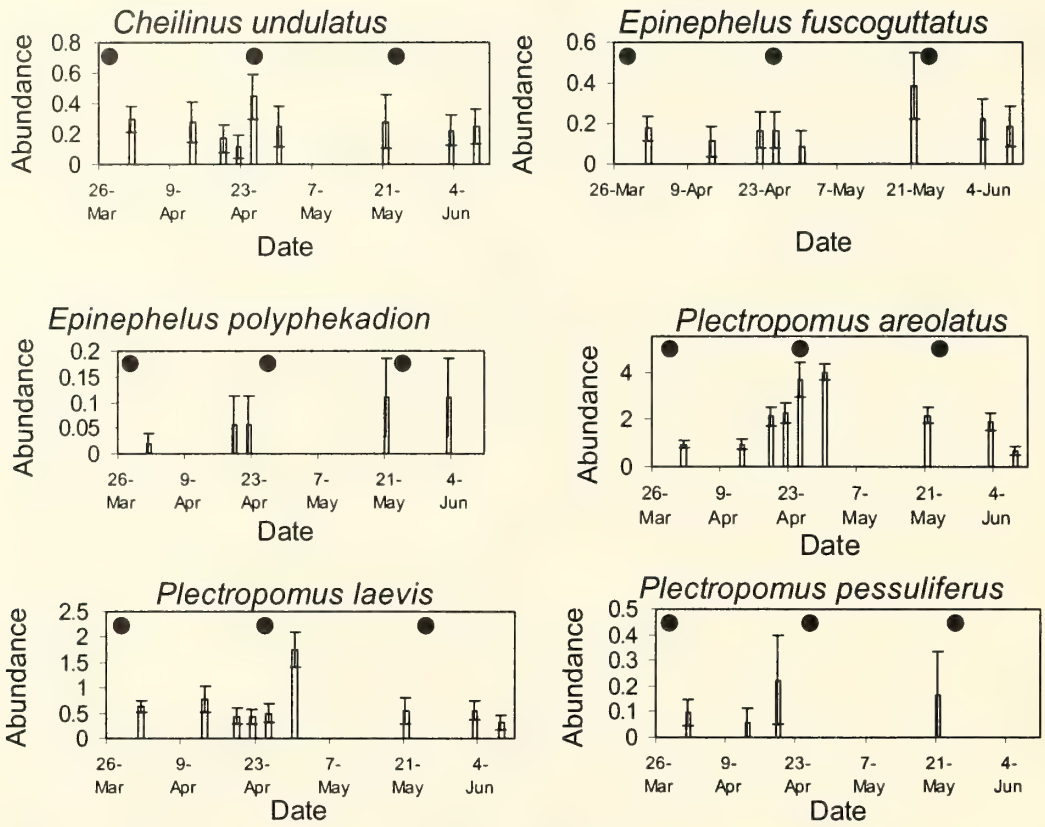

Figure 4: Mean abundance +/- 1SE (no. fish 10-min^{-1}) of each targeted species in Mundoo Channel by date. Dark circles indicate date of new moon.

to assess grouper abundance. This results in greater flexibility in the timing of sampling as well as being able to use many observers so that larger sample sizes can be collected. The linear relationship between sampling time and target species abundance suggests that timed surveys of different duration can be compared by normalizing to a specific duration. More research is needed to confirm this result. But it highly suggestive and would mean that the duration of each timed survey could be tailored to the specific site as long as transect width remains the same. However, nonparametric ANOVA should be used as variances will not be homogeneous between transects of different lengths (T. McClanahan, pers. comm.).

Several studies have linked increases in water temperature with the timing of grouper spawning (Colin, 1992; Tucker et al., 1993; Samoilys and Squire, 1994; Samoilys, 1997). Samoilys (1997) noted that the first increase in *Plectropomus leopardus* on her site in the northern Great Barrier Reef coincided with water temperatures rising about 24°C, which is below the maximum temperature for that region. However, in Maldives, the timing of *P. areolatus* spawning coincided with the warmest month on record and occurred during a time of much coral bleaching. The maximum temperature in Mundoo Channel during the study period at 17 m depth was 32.4°C, while the minimum was 29.3°C (Sluka, 1998). This period of high temperature

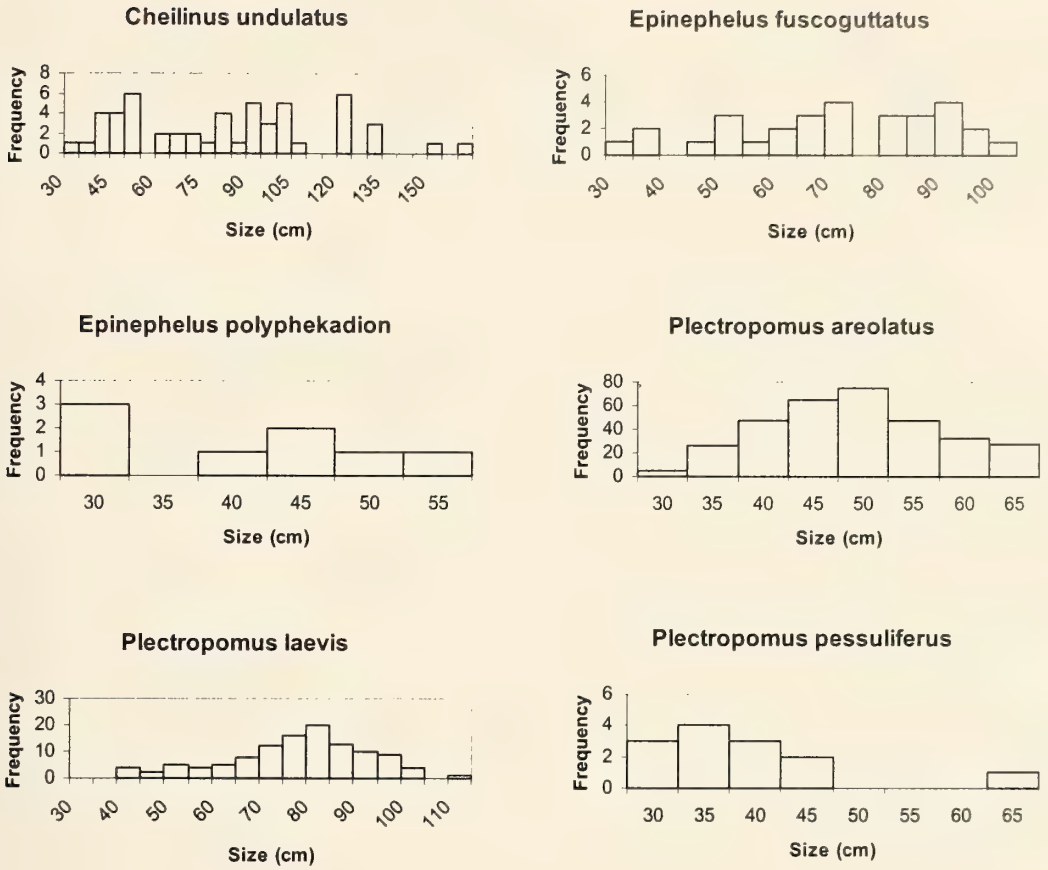

Figure 5. Size-frequency distributions of each targeted species in Mundoo channel.

occurred after the new moon on April 25, but temperatures prior to the new moon were much higher than those previously recorded for the timing of grouper spawning in other countries. This is expected as Laamu Atoll is located close to the equator. The data do not confirm nor contradict the notion that water temperature is linked to the timing of spawning in groupers.

Size data indicate that no small (less than 30 cm) fish were observed in Mundoo Channel. Individuals of this size are rarely observed, but at least one *P. pessuliferus* (approximately 15 cm) was observed on the inner-atoll reef slope off Maabaidhoo Island, which is situated between Mundoo and Fushi channels (Sluka, pers. obs.). It appears that the studied species do not recruit to the channel habitat. Very few small individuals were observed in this atoll (Sluka, 2001). When small individuals of the targeted species were observed, it usually occurred on an inner-atoll reef slope or faro reef slope. Several small (10-20 cm) *P. areolatus* have been observed amongst *Acropora* spp. thickets on the lagoon floor near the inner-atoll reef slope drop off or on the slope itself.

The reproductive ecology of Napoleon wrasse is essentially unknown (Turnbull and Samoilys, 1997). This species will aggregate to spawn in large numbers at sites that appear to be similar to sites where grouper aggregate (Johannes and Squire, 1988; in

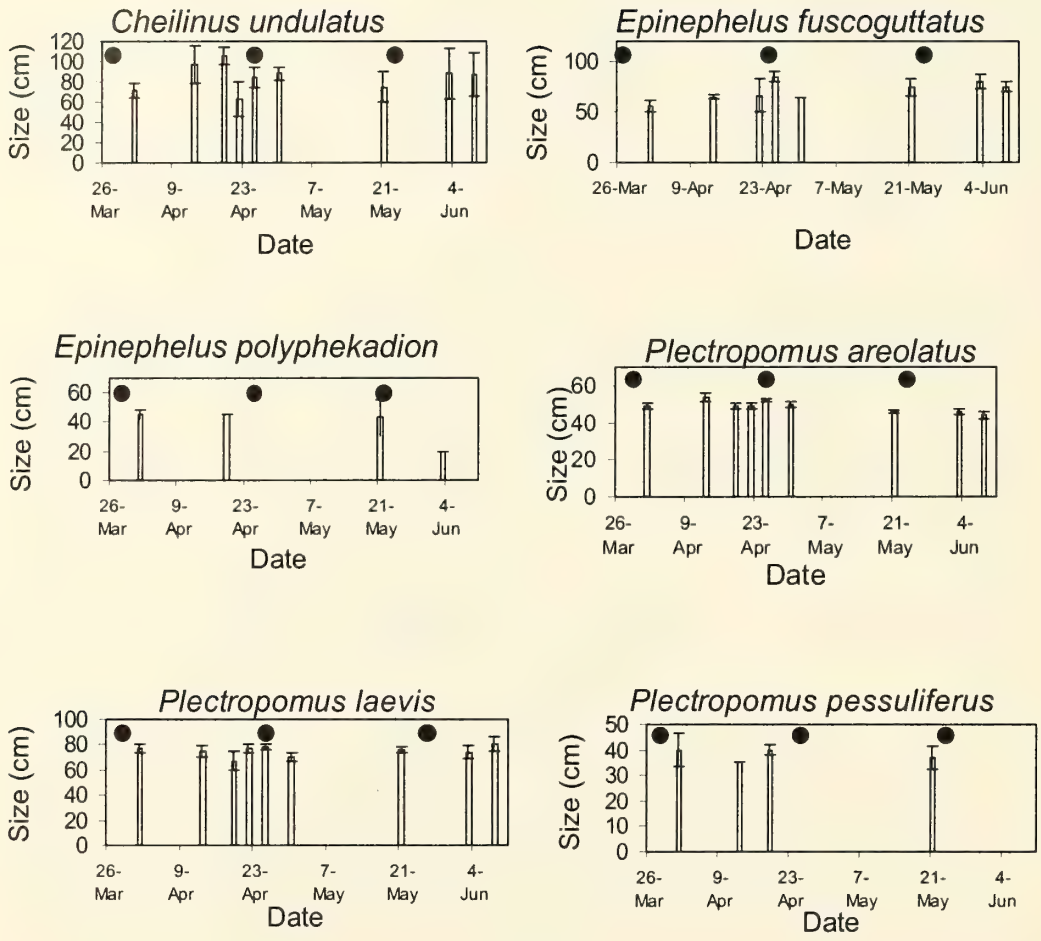

Figure 6. Mean size +/- 1 SE (cm) of target species in Mundoo channel by sampling date. Dark circles indicate date of new moon.

Turnbull and Samoilys, 1997). This species exhibits a parading behavior where individuals will swim in a line, one behind the other (Donaldson, 1995a). However, it is not known if this precedes spawning as spawning has not been observed.

The reproductive ecology of groupers is influenced greatly by the biology and behavior of these species. Most species of grouper are considered to be protogynous (changing sex from female to male at some stage in the life history). However, males may develop directly from juveniles in some species (Sadovy and Colin, 1995). Transition from female to male appears to be socially rather than biologically mediated, as there is a wide range of ages and sizes at which transitional individuals have been recorded (Shapiro, 1987).

Indo-Pacific groupers exhibit a wide variety of spawning patterns including non-migratory pair spawning (e.g. *Cephalopholis spiloparea*, *C. urodeta*), nonmigratory haremic spawning (e.g. *C. argus*, *C. miniata*), and migratory pair and group spawning (e.g. *Epinephelus fuscoguttatus*, *Plectropomus areolatus*, *P. leopardus*) (Goeden, 1978; Johannes,1981, 1988; Shpigel and Fishelson, 1991; Samoilys and Squire, 1994;

Donaldson, 1995b). The migration of large numbers of groupers to specific sites during a few months of the year has been termed a spawning aggregation. Spawning aggregations have been shown to be very predictable in both space and time (Sadovy, 1994; Samoilys, 1997). Individuals gather a few days before the new moon (in the western Atlantic, full moon) at specific locations, many times at the outer end of a channel or promontory, to begin spawning. Spawning aggregations persist for several days around the appropriate moon (Johannes, 1988; Samoilys, 1997). Spawning behavior, such as males nudging the vent of females, occurs throughout the day culminating in external fertilization approximately 10-20 minutes before dusk (Johannes, 1988; Samoilys and Squire, 1994; Turnbull and Samoilys, 1997; Zabala et al., 1997). The eggs are pelagic and spend about a month in the water column before settling to coral-reef habitats (Leis, 1987).

This study cannot conclusively place the target species into any of these categories due to lack of observation data. However, this study does suggest that *P. areolatus* is a migratory pair spawner, rather than a migratory group spawner. Courtship behavior was always observed between two individuals, never more than that. Also, abundance in the channel rose near the new-moon spawning times suggesting migration. Data on *P. laevis* from this study is scant and could be interpreted as nonmigratory haremic or migratory group spawning. This is due to groups of four to five individuals being observed together in Mundoo channel near the new moon, but during no other time. It cannot be confirmed that this species migrated to the channel for spawning. The assessment for this species is highly speculative.

The identification of grouper spawning aggregation sites as well as the timing of the aggregations in Maldives remains an urgent question for research. Research should be focused around the monsoonal shifts. If grouper can be confirmed to spawn during these times in several atolls, this would make a temporal closure of the fishery feasible as it is unlikely that all or most of the grouper aggregation sites in the Maldives will be located in the next several years.

Important questions to answer in regard to the aggregations include:

1) Where and when do the aggregations occur?
2) How much of the population spawns during each aggregation season?
3) What are the movement patterns between home ranges and spawning aggregation sites?
4) How are the sexes distributed throughout the nonspawning season?
5) Do larvae produced in spawning aggregations stay within a particular atoll or is there inter-atoll transfer of larvae?

Armed with this information, a system of marine fishery reserves could be designed to potentially protect grouper within Maldives so that the important live fish-food industry can continue and can be sustainable. However, numerous studies have shown the pervasive negative effect of intense fishing pressure on targeted species (see review in Sluka, 1998). It is clear that marine fishery reserves protect fish biomass, size structure, and reproductive output (Sluka et al., 1997). Several studies have also shown that these reserves export biomass through fish movement to surrounding areas that becomes available for fishers (Russ and Alcala, 1996; Sluka et al., 1997; Zeller and Russ, 1998). Studies on the patterns of larval dispersion via currents are likely to show that marine

fishery reserves are a source of recruits to fished areas (PDT, 1990). It is, therefore, more important to establish marine fishery reserves sooner rather than later when more information becomes available. Once the research questions listed above are answered, the system of reserves can be adjusted to maximally protect the populations. In the short run, however, lack of protection from fishing has been proven to be extremely detrimental to intensely fished grouper populations.

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GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 3. FISHING EFFECTS AND MANAGEMENT OF THE LIVE FISH-FOOD TRADE

BY

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GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 3. FISHING EFFECTS AND MANAGEMENT OF THE LIVE FISH-FOOD TRADE

BY

ROBERT D. SLUKA[1]

ABSTRACT

The live fish-food industry has recently developed in the Republic of Maldives targeting grouper (Pisces: Serranidae) for export to Asian markets. This study uses data collected in one central and one southern Maldivian atoll with the purpose of examining the influence of fishing on these grouper assemblages. Abundance of five grouper species targeted by the live fish-food industry and the Napoleon wrasse (*Cheilinus undulatus*), a targeted species in other countries but banned from export in Maldives, was estimated using timed transects in channel habitats of Laamu Atoll. One site in Kaafu Atoll was resurveyed using the same methods as a previous study four years previously.

Relative grouper abundance was significantly different among channels that experienced different fishing pressure. Channels which had been more intensely fished had lower *Plectropomus areolatus* and *P. laevis* abundance than more lightly fished channels. One site surveyed in 1993 and 1997 showed clear effects of intense fishing pressure. Grouper species composition changed over this time period with targeted species being less abundant in 1997 than 1993. The overall size distribution shifted towards smaller sizes in 1997. Density between the two years was not different, indicating a second-order effect where smaller, nontargeted grouper species increase in abundance once larger species are removed.

Fishing pressure on grouper continues to increase in Maldives and many sites show signs of local overfishing. It is suggested that protecting spawning aggregations within a system of marine fishery reserves and managing nonprotected areas through other measures such as export quotas could result in a sustainable grouper fishery.

INTRODUCTION

The most recent fishery to severely threaten grouper populations is the live fish food trade. Grouper are caught throughout the Indo-Pacific and shipped live to Hong Kong as well as other southeast Asian countries such as Singapore and China. The purchase of high-priced fish is a show of wealth and status in many Asian cultures. Once the grouper populations near Hong Kong were depleted, fishing fleets of small boats set out for the Philippines. Fish buyers from Hong Kong and Singapore now consider the Philippines to be nearly depleted as a source of grouper due to the low number of individuals available for harvest (Johannes and Riepen, 1995). These same buyers

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estimated that Indonesia had three to four more years before it was depleted as a source for grouper. Fishing effort for grouper has intensified, including using larger vessels and fishing farther abroad from the Maldives to the west and east to many of the Pacific island nations.

There can be considerable environmental damage done by fish collectors. In many countries cyanide is used to collect groupers. This poison stuns large fish, but kills both corals and smaller fish (Johannes and Riepen, 1995). Restrictions have been established in many countries, but generally too late and with little enforcement. Given appropriate management, live fish-food fishing can be an important sustainable source of income. However, lack of management and the insatiable demand for live grouper have resulted in the overfishing of many grouper populations in the Indo-Pacific (Johannes and Riepen, 1995).

Maldivians have traditionally relied most heavily on pelagic resources for food and economic livelihood. However, subsistence-level reef-fish fishing has always occurred, especially in atolls which are far from good tuna fishing spots. During bad weather or special times of the year (e.g. fasting month) reef fish constitute the main source of protein for the islanders. In recent years, the demand for reef fish resources by the tourist industry (e.g. lobster, reef fish) and outside markets (e.g. Napoleon wrasse, giant clams, sea cucumbers, groupers) has resulted in the commercialization of reef-fish fisheries (Maniku, 1994). This brings about intense pressure on reef resources due to the high price paid by those external to Maldives. For example, in Laamu atoll, the beach-side price for tuna in 1998 was 3.5 rf per kilogram (11.72 rf = 1 US dollar) while it was 300 rf per kilogram of dried sea cucumber. This provides great incentive to switch to these nontraditional sources of income. These developing fisheries pose two main threats: 1) overexploitation of the resources and 2) conflicts with other user groups (Shakeel and Ahmed, 1996). The main user-group conflict is with tourist resorts which rely on diving to attract many of their customers.

The most recent of these nontraditional reef-fish fisheries is the live grouper trade. The fishery for grouper started about January 1993 (Shakeel, 1994a). Grouper export rose from 200 tons in 1994 to 1000 tons in 1995 (Shakeel and Ahmed, 1996). Exports for 1996 were expected to show about a 10-fold increase above the 1995 level (Mohammed Shiham Adam, Marine Research Section, Ministry of Fisheries and Agriculture, pers. comm.). There are at least 41 species of grouper known from Maldivian waters (Randall and Anderson, 1993; Adam et al. 1998; Anderson et al., 1998). However, only a few of these are targeted commercially. In Laamu Atoll, for example, the highest prices are paid for the *Plectropomus* species, *Epinephelus fuscoguttatus* and *E. polyphekadion* (Sluka, pers. obs.). *Cephalopholis* spp, *Anyperodon luecogrammicus*, and *Aethaloperca rogaa* may fetch one-fifth to one-tenth of the price of the former species. In fact, the *Cephalopholis* species have been used to feed the more expensive species as the exporters did not think it worthwhile to use up hold space on these less expensive species. They continued to buy the *Cephalopholis* spp. from fishermen and cut them up for food. The hold of one vessel (14-ton capacity) was filled with *E. fuscoguttatus* and *Plectropomus* spp. only (Sluka, pers. obs.). The fishery is already showing signs of overfishing. Collectors have shifted away from atolls close to Malé and now have collection sites in all atolls (Mohammed Haleem, Oceanographic Society of Maldives, pers. comm.).

Grouper are collected using small rowboats (1-2 people), sailing vessels (3-4), or large mechanized boats (7-8) (Shakeel, 1994a,b). Sailing vessels may catch 50-80 fish per day, while mechanized boats, 100-170 (Shakeel, 1994a). The fishermen use snorkeling gear and handlines directly from the water. In this manner they can identify individuals they would like to catch and pursue. The preferred bait is the goldband fusilier (*Pterocaesio chrysozona*). A hook is placed through the rear of the fusilier so that it remains alive and swimming, thus attracting grouper. The daily catch of fishermen is then either placed in their own small cages or directly brought to the collector's large cage facility. Shakeel (1994a) estimated a 5-20% mortality rate in boat holds. This is due to poor water quality in holds, overcrowding, and damage to the fish during processing. A number of fish die due to the hook being swallowed resulting in internal bleeding. Another source of mortality is the rapid expansion of the swim bladder due to the fish being pulled rapidly to the surface. The fishermen release the air from the bladder with a sharp tool but may pierce too deeply resulting in internal bleeding.

Grouper are bought from the fishermen by a local collector who acts as a middleman for a foreign exporter (usually from Hong Kong). The price paid to the fisherman depends upon demand (how imminent is the arrival of the foreign collector vessel and what has been the mortality of fish in cages), species, and size. These different groups of fish are held separately in cages approximately 4 x 3 x 2.5 (depth) m in measurement. These cages are generally supported by a framework of metal piping and held afloat by empty plastic fuel barrels. Mortality in cages can be quite high--up to 30% for the *Plectropomus* spp. (Mohammed Afeef, grouper exporter, pers. comm.). The fish are then transferred to a foreign collector vessel at which time the Maldivian intermediary receives monetary compensation.

Shakeel (1994a,b) estimated the maximum sustainable yield of grouper for all Maldivian atolls which totalled to 1,800 tons. For Laamu Atoll, Shakeel (1994a) estimated the maximum sustainable yield of groupers from shallow coral reefs at 27 tons per year. The foreign collection vessels have holds of approximately 14 to 16-ton capacity. These vessels may collect from more than one atoll depending on where the Maldivian intermediary has his collection bases. One vessel collected approximately 7-8 tons of grouper on one trip to Laamu Atoll (Sluka, pers. obs.). Another vessel was already on its way to collect the remaining fish in cages and vessels were expected at least every 6-8 weeks. If we assume that 1-2 collection trips occur every 6-8 weeks, then 42-139 tons would be collected per year. In 1994, fishermen were already reporting that their catches were declining, especially in Alifu and Vaavu Atolls (Shakeel, 1994a). Shakeel and Ahmed (1996) concluded that based on export figures for all Maldives combined (1000 tons) and the mortality rate in fishermen's and exporter's holding facilities, the maximum sustainable yield for grouper was likely surpassed in 1995.

The purpose of this paper is to review the nature of the Maldivian grouper fishery and use data collected under different fishing intensities and durations of fishing pressure to examine the impact of this fishery on grouper assemblages.

METHODS

Abundance surveys

Grouper abundance (no. fish 10 minute^{-1}) was determined for six of the seven channels (see Figure 1 in Part 2 of Sluka, 2001a) leading from the inner-atoll lagoon to the open ocean, at least once, using the same methodology detailed in Part 2 of this series (Sluka, 2001a). Briefly, eighteen 10-minute surveys with a transect width of 10 m were conducted in each sampling session. Mundoo Channel was surveyed nine times between April-June, 1998 while Vadinalhu and Fushi channels were surveyed twice during this same time period (Table 1). The other three channels were surveyed once. A one-way ANOVA was used to test for significant differences in fish abundance among the six channels for each targeted species. A percent similarity index was calculated among all six channels using the abundance of the five targeted grouper species (*Epinephelus fuscoguttatus*, *E. polyphekadion*, *Plectropomus areolatus*, *P. laevis*, and *P. pessuliferus*) and the Napoleon wrasse (*Cheilinus undulatus*). This matrix was used in unweighted, group-average linkage clustering to examine which channels were most similar with regard to targeted species abundance.

Resurvey of sampling site in Kaafu Atoll

Sluka and Reichenbach (1996) reported the results of sampling Gaagandu reef slope for grouper density, diversity, and average size. Gaagandu is a small island near the capitol of Maldives, Male' in Kaafu Atoll, approximately 210 km north of Laamu Atoll. Data were collected in June and July, 1993. This represents the time period when the grouper fishery started in Maldives. Sluka and Reichenbach (1996) showed that fifteen 240 m^2 would capture about 80% of the grouper species diversity and achieve a precision around the median density of about 10%. Thus, sixteen 240 m^2 transects were surveyed at Gaagandu reef slope in March, 1997 to examine the impact of almost four years of fishing on grouper diversity, density, and size distribution. A 20 m transect line was laid haphazardly along one depth gradient. The transect was searched for groupers using a zig-zag swimming pattern, searching in all caves, crevices and holes (GBRMPA, 1978). A width of 6 m was visually estimated out from each side of the transect line. The number and size (nearest 5 cm) of each individual within transect boundaries was recorded. The total number of grouper observed per transect was compared between the two sampling dates using a t-test. Fish sizes were placed in one of five categories to match data in Sluka and Reichenbach (1996): < 5 cm, 6-15 cm, 16-25 cm, 26-35 cm, and > 35 cm total length. A Chi-square test was used to test for significant differences in the size distribution between sampling dates.

RESULTS

Abundance surveys

There was no significant difference in abundance among channels for any species ($p>0.05$) except *Plectropomus areolatus* ($n=282$, $F_{6,275}=2.2$, $p<0.05$) and *P. laevis* ($n=282$, $F_{6,275}=4.8$, $p<0.001$) (Fig. 1). The Tukey test for *P. areolatus* was inconclusive but the test for P. *laevis* showed that it was more abundant in Mundoo Channel than in Gaadhoo Channel or for one of the sampling dates in Vadinolhu Channel,

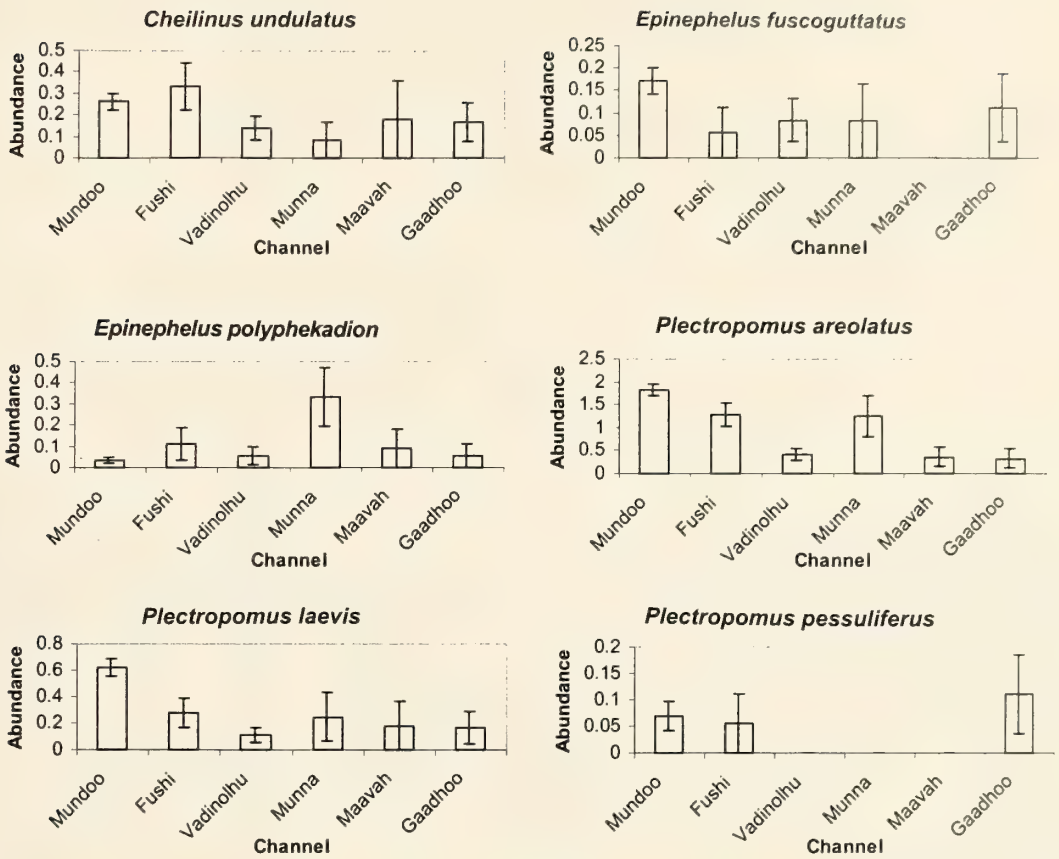

Figure 1. Mean abundance +/- 1 SE (no. fish 10-min^{-1}) of target species in all channels

but similar among all other channels. Figure 2 shows that channels clustered into two groups: Fushi, Munnafushi, and Mundoo channels were most similar as were Gaadhoo, Maavah, and Vadinolhu.

In addition to surveying for targeted grouper species, any grouper species was recorded that was present in the channel. This yielded a species list for each channel (Table 1). A total of 18 grouper species was observed in channel habitat in Laamu Atoll.

Resurvey of sampling site in Kaafu Atoll

Mean grouper density (no. 240 m^2) was not significantly different between 1993 and 1997 ($t=1.299$, $df=35$, $P>0.05$). The mean density in 1993 (1 SE) was 25.2 (1.5) grouper 240 m^2, while in 1997, 22.1 (0.5) (Fig. 3). The size distribution, however, was significantly shifted towards smaller sizes ($X^2= 156.8$, $df=4$, $p<0.001$). Figure 4 shows that there were fewer larger fish, especially greater than 35 cm, in 1997 than in 1993. In 1997 targeted grouper species were rare, with only two *Epinephelus polyphekadion* observed and no *Plectropomus* spp. These targeted species were not abundant in 1993, but were commonly observed. The species composition was similar, with the aforementioned exception. There were 17 grouper species observed in 1993 and 13 in 1997. However, sample size was much higher in 1993 than in 1997, 48 and 16 transects, respectively. When the number of species observed in 1997 is corrected for sample

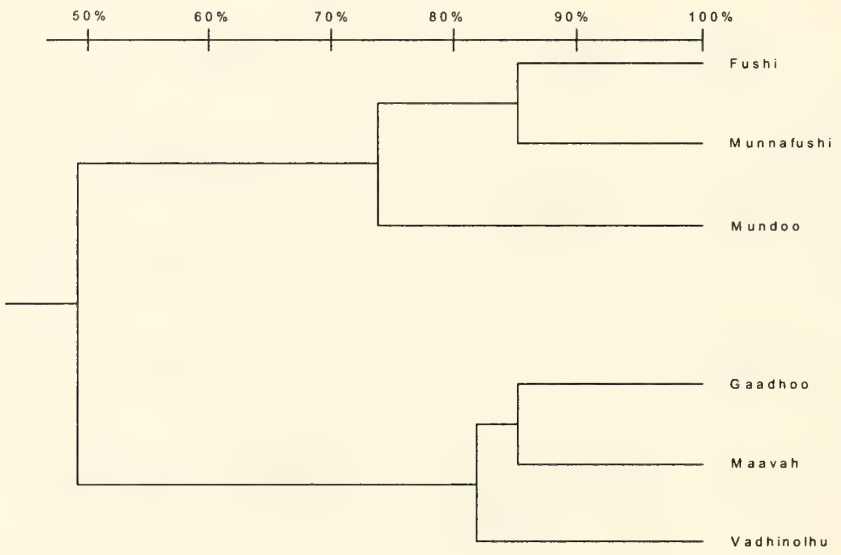

Figure 2. Cluster diagram showing the relationship between all study channels based upon the abundance of targeted species.

Table 1. Grouper species observed in Laamu Atoll channels.

Species	Mundoo	Fushi	Vadinolhu	Munnafushi	Maavah	Gaadhoo
Date surveyed	3/31-6/19[1]	4/26, 5/24	4/23, 6/9	6/9	6/10	5/23
Aethaloperca rogaa		X	X	X	X	X
Anyperodon luecogrammicus	X	X	X		X	X
Cephalopholis argus	X	X	X		X	X
C. leopardus	X		X			
C. miniata	X	X	X		X	X
C. sexmaculata	X					
C. urodeta	X	X	X	X		X
Epinephelus caeruleopunctatus	X				X	X
E. fasciatus	X					
E. fuscoguttatus	X	X	X	X	X	X
E. polyphekadion	X		X	X		X
E. spilotoceps	X		X			X
E. tauvina	X					
Gracila albomarginata	X	X	X	X	X	X
Plectropomus areolatus	X	X	X	X	X	X
P. laevis	X	X	X	X	X	X
P. pessuliferus	X					
Variola louti	X		X	X	X	X

[1]This channel sampled multiple times during this time interval.

size using the graph in Sluka and Reichenbach (1996), 16 species can be assumed to be present in 1997.

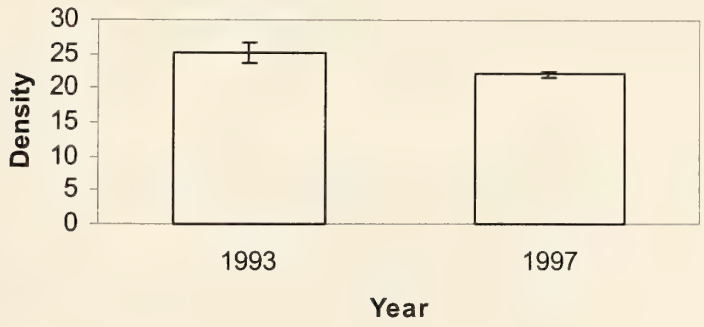

Figure 3. Mean grouper density (all species combined, no. 240 m^{-2}) for two separate years at Gaagandu Island, Kaafu Atoll.

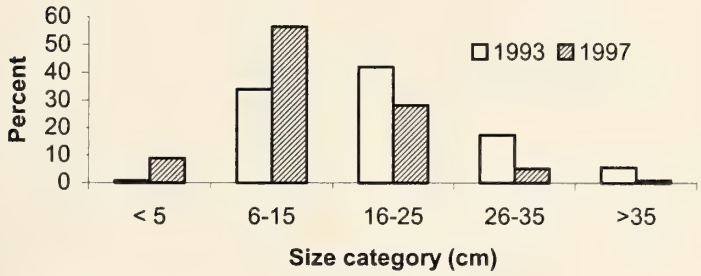

Figure 4. Size-frequency distribution of all grouper species combined for two different years at Gaagandu Island, Kaafu Atoll.

DISCUSSION

Grouper species diversity was similar to that found in a previous study in Laamu Atoll (Sluka 1998). A total of 18 grouper species in seven genera were observed in this study, while 25 species in seven genera were identified by Sluka (2001b). Both counts are much less than the total number observed for all Maldives of 41 (Randall and Anderson, 1993; Adam et al., 1998; Anderson et al.,1998). The main species differences between channels surveyed in this study and the previous study by Sluka in Laamu Atoll were in fewer small, cryptic and rare species. This could be due to lower sampling time or related to habitat differences among channels and other types of reefs. Sluka (2001b) found 19 grouper species on reef slopes on the ocean side of the atoll, 24 on reef slopes inside the atoll rim, 17 on faros, and 3 in lagoonal habitats. Channel habitat grouper diversity was most similar to outer-reef slopes and least similar to lagoonal habitats.

Data from all channels indicate two separate groups of channels cluster together: deeper, more intensely fished channels and shallow, less intensely fished channels. While there is currently only one grouper-collection site in Laamu Atoll (located on the island of Kashi Guraidhoo, next to Maavah Channel), in the past several years there was another site located near Maamendhoo which is next to Gaadhoo Channel. Grouper fishermen from Laamu and other atolls bring their fish to these sites and sell them to the grouper collectors. According to local villagers, much of the fishing for grouper in the past several years has been conducted on the western side of the atoll which includes the areas around Kashi Guraidhoo and Maamendhoo. Figure 2 shows that *Plectropomus areolatus* and *P. laevis* abundance was lower in these more heavily fished channels than

in less intensely fished channels. Munnafushi Channel (also located on the western side of the atoll) is a shallow channel (approximately 10 m depth) with extremely high current speeds (pers. obs.). These physical differences likely account for less fishing pressure in this channel. These data reinforce the already overwhelming evidence that intensive fishing results in sites with significantly decreased grouper abundance relative to unfished sites (see Sluka, 1998 for a review).

Resurvey of sampling site in Kaafu Atoll

It appears that fishing pressure at the site near Gaagandu Island has resulted in a shift in species composition and size distribution, but not in mean density. This may indicate compensation, the so-called second order effect shown by other researchers (Bohnsack, 1982; Goeden, 1982; Watson and Ormond, 1994; Sluka et al., 1996; Sluka and Sullivan, 1998). When larger grouper species are removed, smaller species become more abundant. This may be due to a reduction in competition or predation, but no experimental evidence is available to suggest the most likely mechanism for this occurrence. Bohnsack (1982) found that graysby were more abundant in sites unprotected from spear-fishing than in protected sites. Watson and Ormond (1994) found that the relative contribution of smaller *Cephalopholis* spp. was significantly greater in sites unprotected from artisanal fishing than in those protected. Grouper species in an unexploited condition may significantly compete for resources intra- and interspecifically. The release of this competition and/or predation may allow the smaller species to increase in abundance due to the increase in resources available to them. There are no data that I am aware of to suggest that larger grouper species are preying on smaller grouper species (Randall, 1967; Randall and Brock, 1960; Kingsford, 1992). Stomach contents of *Epinephelus merra* (n=481), *Cephalopholis argus* (n=280), *C. miniata* (n=48), *C. urodeta* (n=71), and *Plectropomus leopardus* (n=7) contained no grouper (Randall and Brock, 1960).

The shift in size distribution from larger average size in 1993 to smaller average size in 1997 is likely due to the direct effects of fishing. In 1997 no Plectropomid species were observed. These species are among the most highly sought after for the live fish-food trade. While these species were not abundant in 1993, they were regularly observed. Data from Sluka and Reichenbach (1996) underestimated the abundance of the *Plectropomus* spp. due to using fixed area transects. These species are highly mobile and are more amenable to sampling using timed counts (Newman et al., 1997). This shift in species composition and size distribution is consistent with shifts observed in other grouper populations subjected to heavy fishing (Russ, 1985; Russ and Alcala, 1989; Sluka et al., 1997; Sluka and Sullivan, 1998).

Effects of fishing on grouper populations

Intensive fishing for grouper results in a population that has different characteristics than an unexploited population. Grouper in fished areas, relative to unfished ones, tend to be smaller in average size, less dense, and collectively produce fewer eggs. There are also significant genetic changes where fishing selectively removes individuals with particular life history features such as large size. Sixteen grouper species were recommended for inclusion in the IUCN Red List of Threatened Animals (Hudson and Mace, 1996). Most of these species are the larger groupers, which are the

target of commercial and recreational fisheries. The largest of all grouper species, the giant grouper *Epinephelus lanceolatus*, is included in the proposed list and occurs in Maldives.

The growth and reproductive characteristics of groupers render these species especially susceptible to overfishing (Shapiro, 1987; Bannerot et al., 1987; Huntsman and Schaaf, 1994). Groupers which are targeted by fishing generally grow slowly to a large maximum size (Manooch, 1987). The removal of larger individuals leaves behind smaller individuals to spawn. Over many generations, this can result in a decrease in the size/age at sexual maturity (Ricker, 1981) and also decrease the average size of the population (Roberts and Polunin, 1991). Fishing pressure can cause genetic shifts in the age/size at first reproduction, growth rate and decrease the genetic variation in the population (Sheridan, 1995).

Many grouper species are protogynous hermaphrodites, changing sex from females to males later in life (Shapiro, 1987). Larger groupers are generally males, and at intensive fishing levels, the number of males in the population can be drastically reduced. If too many males are removed, sperm can become limited for reproduction (Bannerot et al., 1987). If sperm is limited, protogynous stocks are more vulnerable to overfishing than gonochoristic stocks (Huntsman and Schaaf, 1994). Species which are protogynous may experience a drastic reduction in reproductive capacity, even at moderate levels of fishing (Huntsman and Schaaf, 1994). In addition to protogyny, the reproductive behavior of groupers may increase their susceptibility to overfishing.

Many species of grouper aggregate to spawn in one or two months of the year. Grouper spawning aggregations are the focus of commercial, recreational, and artisanal fisheries throughout subtropical and tropical regions of the world (Olsen and LaPlace, 1978; Johannes, 1988). Groupers appear to be especially susceptible to overfishing at this time due to: 1) behavioral changes rendering them less wary of fishers; 2) fishing of spawners prior to gamete release; 3) selective removal of larger males, potentially resulting in sperm limitation (Bannerot et al., 1987); 4) aggregations returning to the same place at the same time each year; 5) concentration of populations. Intense fishing of grouper spawning aggregations has lead to decreases in abundance and mean size of individuals as well as strongly female-biased sex ratios (Sadovy, 1994; Coleman et al., 1996; Koenig et al., 1996). This results in reduced average fecundity of the population and, ultimately, decreased population size, reduced population growth, and extinction (Coleman et al., 1996). Extinction could be economic, as there are too few individuals of a species for a fishery to exist--locally due to a lack of any individuals at a particular site, or regionally because of a lack of any individuals of a species anywhere.

Coleman et al. (1996) have shown that the nature of a grouper species' reproductive behavior influences their susceptibility to fishing pressure. For example, two heavily fished species in the Gulf of Mexico that migrate to spawn in aggregations and have spatially segregated sexes (i.e. males and females live in different places throughout the year) had severely reduced sex ratios. However, in the same location, a species where males and females have access to each other throughout the year, and do not aggregate to spawn, have not had marked size or sex ratio changes in the past 25 to 30 years, despite intensive fishing pressure. It is thus imperative to understand the reproductive ecology of the species sought after in the live fish-food trade. The two *Epinephelus* species studied herein, *E. polyphekadion* and *E. fuscoguttatus*, have been

shown to aggregate to spawn in other places (see review by Domeier and Colin, 1997). Similarly, Plectropomids have been observed to aggregate for spawning in other studies (Goeden, 1978; Johannes, 1988; Samoilys and Squire, 1994). Part 2 of this study (Sluka, 2001a) indicates that *Plectropomus areolatus* aggregates to spawn in Maldives, based upon a three-fold increase in numbers at a spawning site (Samoilys, 1997). It is not known how the separate sexes are distributed spatially. According to Coleman et al. (1996), if these species were able to judge the population sex ratio throughout the year (i.e. sexes not spatially segregated), intense fishing would not alter population sex ratios. If the only time a female can judge the population sex ratio, and thus determine whether or not to change sex to a male, is during the spawning aggregation, then intense fishing pressure would significantly alter population sex ratios. In either case, aggregating species are highly susceptible to local extinctions (Coleman et al., 1996). In some cases, aggregations that were successfully fished artisanally have disappeared due to the increased pressure brought about by gear improvements or outside markets.

Little is known about how many times an individual grouper will travel to an aggregation in one spawning season or how far an individual generally swims to arrive at these points. Johannes et al. (1995) in Zeller (1997) observed an individual *Epinephelus polyphekadion* in Palau travel 10 km to an aggregation site. Tagged Nassau grouper (*E. striatus*) have been shown to migrate to spawning aggregations up to 110 km (Colin, 1992) and 240 km (Carter et al., 1994) distant in the Bahamas and Belize, respectively. However, Samoilys and Squire (1994) found aggregation sites for the grouper *P. leopardus* as close together as 1 km. In addition, both Samoilys (1997) and Zeller (1997) found smaller aggregations near the primary aggregation sites. Thus, it is unknown how many aggregation sites occur in an atoll. If there is only one site per atoll and this site is heavily fished during the aggregation time, the entire reproductive output for the atoll could be diminished to the point where the population could not sustain itself and abundance levels would fall to the level of being economically extinct. However, recent research by Zeller (1997) suggests that not all sexually mature *Plectropomus leopardus* traveled to spawning aggregation sites. He suggested that, if less than a third of the population moves to spawning aggregations during the spawning season, this species may be more resistant to overfishing than other grouper species.

Management options

The Maldivian grouper fishery is under considerable stress. There is currently fishing for grouper in all atolls. Grouper exporters complain about reduced abundance and smaller individual sizes in some atolls. This study also showed that fishing pressure is negatively influencing the relative abundance of targeted species in Laamu Atoll and that the size distribution and species composition of groupers at one site in Kaafu Atoll have been significantly reduced and altered towards smaller sizes and fewer commercially important individuals. These are classic signs of intense fishing pressure. Adam et al. (1997) noted that the grouper fishery is rapidly expanding and that a pattern has been established of overfishing one atoll and then moving on to overfish the next. Clearly, based upon the experience of other countries and the present state of development of the Maldivian grouper fishery, management action is necessary. Research suggests that the best management strategy for both maintaining grouper fisheries and conserving natural population size, structure and diversity is to protect

grouper spawning aggregations within a series of marine-protected areas (Sadovy, 1994; Turnbull and Samoilys, 1997). Sadovy (1994) noted that protecting spawning aggregations alone may not be sufficient to prevent overfishing. The management strategy most likely to succeed in both maintaining a population that can sustain substantial fishing pressure and avoiding overfishing focuses on both the spawning and nonspawning times and areas. Spawning aggregations should be closed to fishing, either by permanently closing these areas to fishing or using temporal closures surrounding the time of spawning. The population should also be managed during nonspawning times using methods such as marine fishery reserves, quotas and/or size limits. Fifteen dive sites have been designated as marine-protected areas where fishing activity is banned. However, these sites are small, only located in three atolls, and regulations are not enforced (Adam et al., 1997).

Fisheries management regulations can basically be divided into two categories: controlling the amount of fish caught or the effort used to catch them. Managers throughout the world have used a variety of regulations within these two categories including limiting the total number of grouper caught and the individual or collective weight of an individual fisherman's catch. Effort limitations include restricting gear types, seasonal or spatial closures to fishing, and requiring gear to be less efficient.

Shakeel and Ahmed (1996) made several suggestions for the management of the Maldivian grouper fishery: 1) limiting fishing in each atoll; 2) limiting export; 3) closed areas (but not necessarily permanently closed); 4) size restrictions; 5) improved data collection; 6) aquaculture.

The potential yield of grouper for each atoll was calculated by Shakeel (1994b). He gives a total maximum sustainable yield for the whole country of 1,800 t, a figure which was likely reached in 1995. The problem with using this method, as pointed out by Shakeel, is that there is a variable and significant grouper mortality before export and no method of collecting species-specific data, and the accuracy of the yield estimate is in question. There is already a problem of fishermen moving to other atolls to catch grouper and this would likely cause more tensions between atolls with low quotas and those with high quotas. Quota systems are a common means of managing grouper fisheries, but appear, based on the fact that grouper populations are almost universally overfished, to be ineffective as a management system for these species. While theoretically sound, catch quotas are dependent upon detailed biological and catch data as well as efficient enforcement. Practically speaking, quotas are usually surpassed before the statistics are collected that show the quota has been reached.

Export could be stopped once the maximum sustainable yield is reached. However, this method is dependent upon timely and accurate data collection. This method could be rendered ineffective by significant poaching, lack of data, and/or mortality due to catching, handling, or holding procedures (Wilson and Burns, 1996; Shakeel, 1994a,b).

Limiting the number and/or size of fish collected can easily be rendered ineffective due to significant mortality of undersized fish (Wilson and Burns, 1996). Measures such as effort limitation and size limits are unlikely to rehabilitate overfished grouper stocks (Huntsman and Schaaf, 1994). For example, size limitation is complicated by release mortality (Huntsman and Schaaf, 1994). Groupers brought up from relatively deep water (>30 m) suffer injury and likely mortality from the expansion

of the swim bladder and other internal air cavities. Wilson and Burns (1996) showed that the survival rate of undersized grouper caught deeper than 44 m was less than 33%. They concluded that this rate is too low for the size limit in place to be effective in increasing yield. Render and Wilson (1996) showed that the mortality rate of snapper brought from 21 m depth to the surface and then released (either with the gas bladder inflated or deflated) was 20%. It appeared that there was a higher, but variable, mortality rate in fish caught deeper than 21 m. They concluded that gas bladder deflation did not significantly reduce mortality and may introduce another source of mortality when not performed properly.

Marine fishery reserves

Coral-reef fisheries are usually managed by limiting catch and/or effort. However, grouper populations throughout the world have shown drastic changes in their population structures despite these management measures (Sadovy, 1994). One management option that has been proposed to combat overfishing of coral-reef fish stocks is to establish marine fishery reserves (MFRs) (PDT, 1990). The Plan Development Team (1990) defined MFRs as "areas permanently closed to consumptive usage". The benefits of MFRs are numerous and include protecting the age structure of the population, maintaining genetic variability, and providing brood stock to replenish other areas. Based on previous experience with MFRs throughout the world, it is expected that MFRs will have similar beneficial effects on any reef-fish populations.

Several reviews of the benefits and design of marine fishery reserves have recently been completed (PDT, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994). Marine fishery reserves result in a higher abundance and larger commercial species in the reserve than outside the reserve and protect the spawning stock biomass of these species (Russ et al., 1993).

There are two general means by which reserves benefit local fishermen in terms of increased catch: larval transport and spillover of adults. Little research has been carried out on these two processes. Most coral-reef fish have a bipartite life cycle with relatively sedentary adults and pelagic larvae (Sale, 1991). The fecundity of fish is related exponentially to their length, so that a large fish may reproduce hundreds of times as much as a fish half its size (PDT, 1990). Adults spawn eggs that are buoyant and float downstream on the prevailing current patterns. These eggs develop and settle in areas that are fished, thus replenishing those populations. While adults are relatively sedentary, a certain percentage of the population will make large-scale movements in a short period of time and many of the adults will move distances of several miles throughout their lives (PDT, 1990). The movement patterns of a porgy (*Coracinus capensis*) in South Africa were studied by tagging and releasing individuals (Attwood and Bennett, 1994). Over several years, they found that 17.8% of the tags were returned outside of the reserve. Those found outside of the reserve had moved a minimum of 25 km and a maximum of 1044 km. This is similar to most tagging studies in which most individuals of sedentary-type fish remain in a small area with a few nomads that travel long distances. Through the movement of adults out of the MFR, the yield to fishermen along MFR edges is increased. Sluka et al. (1997) showed that mean Nassau grouper density was higher in the 5 km adjacent to the park than at distances farther from park boundaries.

CONCLUSION

Management of the live grouper trade in Maldives is urgent. Evidence from around the world suggests very strongly that unmanaged or improperly managed grouper fisheries will become overfished quite quickly. There is already evidence of over-fishing in Maldives and the fishery is only four to five years old. Several management options are available. Scientific evidence suggests that protecting a significant portion of the coastal habitat in marine fishery reserves is the best management option for both the resource and resource users. Reserves designed for grouper management need to protect spawning aggregations. As a prelude to a reserve system, the banning of fishing grouper spawning aggregations would provide the next best strategy for long-term use of the resource. Given the current lack of a detailed data-collection system for reef species (Shakeel and Ahmed, 1996), it is unlikely that limiting catch or export using maximum sustained yield figures will provide long-term protection for the resource and resource users.

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